REVISION OF *PALICOUREA* (RUBIACEAE: PSYCHOTRIEAE) IN THE WEST INDIES

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Taylor, Charlotte M. (Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299, U.S.A.). Revision of *Palicourea* (Rubiaceae: Psychotrieae) in the West Indies. Moscosoa 7: 201-241. 1993. A revision is presented of the eight species of *Palicourea* found in the West Indies, excluding Trinidad and Tobago. *Palicourea* crocea Swartz is recognized as a species separate from *P. croceoides* W. Hamilton (= *P. riparia* Bentham), *P. barbinervia* de Candolle is combined with *P. guianensis* Aublet, and *P. eriantha* de Candolle of Hispaniola is recognized as separate from, but most closely related to *P. alpina* Swartz. Distyly appears to have been lost independently in at least three of the island species. These plants most likely reached the islands by over-water dispersal.

El género *Palicourea* (Rubiaceae: Psychotrieae) en el Caribe. Se presentan descripciones y una clave de las ocho especies de *Palicourea* de las Antillas con exclusión de Trinidad y Tobago. Se separa *P. crocea* Swartz de P. *croceoides* Hamilton (= *P. riparia* Bentham), se combina *P. barbinervia* de Candolle con *P. guianensis* Aublet y se considera *P. eriantha* de Candolle de La Española separada, aunque estrechamente afín, de *P. alpina* Swartz. La condición de distilia parece ser perdida independientemente en tres especies isleñas. Estas plantas llegaron a las Antillas más probablemente por dispersión sobre el agua.

Palicourea Aublet includes about 200 species of neotropical shrubs. The characteristics of the genus, including its separation from *Psychotria* Linnaeus, have been described elsewhere (Taylor, 1989). The present study is a second installment toward a revision of the genus, covering the species found in the Greater and Lesser Antilles excluding Trinidad and Tobago.

Eight species of *Palicourea* are found in this area. Four of these, *P. crocea* (Swartz) Roemer & Schultes, *P. guianensis* Aublet, *P. croceoides* W. Hamilton, and *P. triphylla* de Candolle, are widespread species that are also found in Central and South America. These four species occur on several islands at relatively low elevations (sea level to ca. 1300 m). The other four *Palicourea* species are endemic to the grater Antilles. *Palicourea alpina* (Swartz) de Candolle and *P. eriantha* de Candolle are found at relatively higher elevations (ca. 700-2200 m), *P. alpina* on all four islands but *P. eriantha* only in Hispaniola. *Palicourea pulchra* Grisebach and P. wilesii C.D. Adams are restricted to relatively low elevations (ca. 300-900 m) in Jamaica.

The West Indian *Palicourea* species are characteristic of moist and wet forests (sensu Holdridge, 1967, and Ewel & Whitmore, 1973), but some grow also in mesic microsites within dry forests. The "higher elevation" Antillean species are generally restricted to cloud and ridgetop forests, although they occur at lower elevations than mainland "montane" species because of the relative compression of elevational zones on islands (Grubb, 1971).

The Antillean species of *Palicourea* have been treated together only by de Candolle (1830) and Grisebach (1861). More recent consideration has been only in floristic treatments of individual islands or island groups (Adams, 1972; Alain, 1962; Barker & Dardeau, 1930; Britton & Wilson, 1925; Duss, 1897; Fournet, 1978; Grisebach, 1857, 1866; Howard, 1989; Jennings, 1917; Liogier & Martorell, 1982; Little et al., 1974; Moscoso, 1943; Sauvalle, 1873; Stahl, 1937; Urban, 1911, 1921).

Reproductive Biology

Most species of *Palicourea* are distylous (Grisebach, 1864; Sobrevila et al., 1983; Taylor, 1989), although a few exceptions have been noted (*P. alpina* in Jamaica, Tanner, cited in Sobrevila et al., 1983; *P. guianensis* in Central America, Taylor, 1989). Most other genera in this tribe are predominantly distylous, including *Psychotria*, the closest relative of *Palicourea*. Therefore distyly is here regarded as ancestral in *Palicourea*.

Two West Indian *Palicourea* species, *P. crocea* and *P. croceoides*, are distylous. These resemble conspecific mainland populations and other mainland *Palicourea* species (Sobrevila et al., 1983; Taylor, 1989) in their floral morphology. The two floral forms differ in style, stigma, anther, and filament lengths, and in pollen size, although apparently not in corolla or anther size. The self-compatibility and morphology of these species appear to follow the general distylous pattern of high intramorph incompatibility (Melampy, unpub.).

The remaining six Antillean *Palicourea* species are monomorphic. These all produce viable fruit from some of the flowers on most inflorescences, and therefore appear to show a loss of the ditylous breeding system, including the intramorph incompatibility (apomixis is an alternative explanation that has not been explored but seems unlikely given the partial fruit set observed). Because these species seem to represent several lineages that are not closely related to each other, the loss of distyly appears to be parallel. This in turn suggests strong selective pressure for the loss of the obligate outcrossing mechanism in the island plants, favoring self-compatibility in the colonizing populations. This loss is presumed to be correlated with colonization of the Antillean islands, similar to the sequence worked out by Baker (1966) in heterostylous and monomorphic Plumbaginaceae.

In five of the monomorphic species, the flowers resemble the long-styled floral form of distylous species in the position of their anthers and stigma (Figs. 2, 9). The monomorphic flowers of *Palicourea pulchra* are generally "long-styled" (Fig. 7) but differ from the distylous long-styled form in their longer exserted style and the anthers also exserted on relatively long filaments. They thus appear to represent a relatively derived floral morphology.

Palicourea flowers in Puerto Rico are visited by hummingbirds (Melampy, unpub; C. M. Taylor, pers. obs.), which are presumed to be the principal pollinators. Bees have also been observed visiting the flowers on occasion (C. M. Taylor, pers. obs.), and Bananaquits (*Coereba flaveola*) frequently make a small hole at the base of the flower to

rob nectar (C. M. Taylor, pers. obs.). The flowers disperse pollen and apparently have receptive stigmas for only one day, although they frequently persist on the inflorescence for another day. Second-day flowers frequently become duller and flushed with orange or brown. Development of fruit requires approximately 8 to 10 weeks. The fruits are succulent and blue-black when ripe, although they are insipid and usually not at all or only slightly sweet. Dispersal is most likely by birds. Anoline lizards also eat succulent fruits, and may be another consumer of *Palicourea* fruits in the Antilles, although this has never been observed. In Puerto Rican *P. croceoides*, fruits are normally produced more or less throughout the year, but no fruit removal by frugivores has ever been seen under normal conditions (Melampy, unpub.; C. M. Taylor, pers. obs.). However, during the period immediately following Hurricane Hugo in the fall of 1989, *Palicourea croceoides* quickly flowered at greater than normal frequency, and soon produced some of the few fruits available in the damaged eastern forests. These fruits were heavily utilized by several species of birds (Wunderle, unpub.; C. M. Taylor, pers. obs.). Dispersal may thus be occasional but intense; after the hurricane, most birds soon moved to less damaged areas in other parts of the island. Larger birds are known to move between islands, and may be effective inter-island dispersers. Many of the Antillean species of *Palicourea* are weedy and widespread where they occur, and their distribution is most likely limited by lack of habitat rather than by inefficient dispersal.

Colonization of the Antilles by *Palicourea*

The species of *Palicourea* in the Antilles do not appear closely related to each other, with the exception of *P. alpina* and *P. eriantha*. The island plants appear to represent descendants of several lines of colonizing predecessors from both Central and South America, as conspecific populations or as endemic species derived from such populations. The putative relationships of the individual species are discussed after each description and summarized in Fig. 1.

The island plants are most likely derived from mainland populations rather than the reverse. This is suggested by the distribution of the majority of *Palicourea* species, including the putative closest relatives of all the Antillean species and their putative sister groups as well, in mainland South and Central America and the presence of distyly, an ancestral condition, in nearly all of the mainland species in contrast to its absence in most of the island species.

Colonization of the Antilles was most likely by dispersal between islands, probably facilitated by birds. Recent geological models of the Caribbean suggest that the Lesser Antilles (except Trinidad and Tobago) have not been connected by land to South America (Pindell & Dewey, 1982). The Greater Antilles are thought to have existed as continuously emergent islands since at least the Oligocene (Pindall & Dewey, 1982; Buskirk, 1985). Unfortunately, the place and geological time of origin of *Palicourea* are unknown, and will likely remain so because the pollen of most species has at best only sparse exine deposits (Taylor, 1989). Studies of sediments in Puerto Rico do suggest that an appropriate climate, similar to that enjoyed by present-day species of *Palicourea*,

prevailed during Oligocene times (Graham & Janzen, 1969). Then or slightly later seems to be the period of colonization of the Antilles by animals (Pregill, 1981).

The breeding biology of present-day Antillean *Palicourea guianensis* suggests one possible pattern and time of movement. This species today is known from throughout Central and South America and the Greater Antilles, and on St. Thomas, Grenada, and Trinidad. The plants of South America are distylous, but those of Central America and the Greater Antilles are monomorphic. The absence of distyly in the Central American and Antillean plants suggests that an island environment prevailed at the time *P. guianensis* moved into this area, possibly (at the earliest) in Oligocene times when the present-day Greater Antilles were the principal islands and from them to Central America, or (at the latest) in later Oligocene to Miocene times when the present-day Central American lands were an island chain and thence into the Greater Antilles. It seems less likely that *P. guianensis* colonized successive islands in the Lesser Antilles, even when the chain lay further west, and from there moved into Central America: in this case, the species was subsequently eliminated from all but the southernmost of that island chain, although the dry climates of the Pleistocene could have caused this. The Grenada locality is represented by one long-styled collection, so its breeding system is not evident; *P. guianensis* could have arrived on this island from nearby Trinidad relatively recently.

Palicourea alpina has a modern distribution similar to that of *P. guianensis*, excluding Grenada. It seems most closely related to Central American plants, and thus probably followed the second route proposed above. *Palicourea eriantha* is found only in Hispaniola, and seems most closely related to *P. alpina*: this species probably evolved in situ.

The mainland ranges of *Palicourea triphylla* and *P. crocea* are similar to that of *P. guianensis*, and both species are distylous throughout their mainland ranges. *Palicourea triphylla* is found only in central and western Cuba, where it appears to have monomorphic flowers. In this case the second colonization route proposed for *P. guianensis* seems most likely. *Palicourea crocea* is found on all four of the Greater Antilles, where it is ditylous, similarly to mainland plants. Based on the evidence at hand, this species could have followed either of the routes proposed for *P. guianensis* with equal probability.

Palicourea croceoides is found throughout the Lesser Antilles and in the Virgin Island, Puerto Rico, and eastern Hispaniola. It nearly complements *P. crocea* in geographic range, and most likely dispersed northward through the Lesser Antilles from its continental range in eastern South America. *Palicourea croceoides* is sympatric with *P. crocea* in Puerto Rico and eastern Hispaniola, and may be expanding its range westward. It is ditylous throughout the Antilles. These two lowland species are widespread common shrubs, in contrast to *P. guianensis*, which is markedly less commom with the mature trees often rather widely dispersed. This difference in population size and distribution may help explain the difference in breeding systems.

Land connections between some islands have been suggested during Pleistocene times of climatic drying and warming (Buskirk, 1985; Pregill & Olson, 1981). These land connections are thought to have been vegetated with dry forest or thorn scrub, and

movement of mesophilic *Palicourea* by this route is unlikely. On the contrary, the distribution of these mesophilic species was probably restricted as the area of wetter fores contracted, with subsequent dispersal into re-expanding moist forest. Even more recently, several islands of the Lesser Antilles have experienced volcanic activity. St. Vincent was covered with several meters of volcanic ash in one event about 40,000 years ago, so the plants of *Palicourea croceoides* found on this island today clearly arrived by inter-island dispersal. In spite of its dispersal abilities, the range of this species in the Lesser Antilles is probably more restricted today than 200-400 years ago, when the forests of many islands were cut for cultivation of cane. Forest area is more restricted today, and in addition the islands have probably become dominated in historical times by more xerophytic vegetation, either as a result of soil degradation or because of declining rainfall in this period (Colón, 1989) (these may not be independent factors).

Taxonomy

The methods used here are similar to those presented by Taylor (1989). Specimens were examined form A, BM, DUKE, F, G, GH, JBSD, K, M, MAPR, MO, NY, P, S, SJ, UPR, UPRRP, US, and WIS. Field observations were made in Puerto Rico, Dominica, the Virgin Islands, and the Dominican Republic. All specimens seen are cited for the less commonly collected or frequently misidentified species, but only selected exsiccatae are listed for *Palicourea alpina*, *P. crocea*, *P. croceoides*, and *P. eriantha*. A complete index to numbered exsiccatae arranged by principal collector and collection number is appended. A complete list of exsiccatae of the four more commonly collected species, arranged by locality, is available on request from the author.

PALICOUREA AUBLET, HIST. PL. GUIANE 1: 172, T. 66. 1775.

TYPE: *Palicourea guianensis* Aublet.

The genus has been described elsewhere (Taylor, 1989).

Key to Species of *Palicourea* in the West Indies

1. Stipule lobes rouded; leaf blades 5-13 (24) cm wide.....5. *P. guianensis.*
1. Stipule lobes acute; leaf blades (1.2) 1.5-9 cm wide.
2. Inflorescences blue to violet, corollas blue; calyx lobes 1-3.5 mm long; plants of Hispaniola, 700-2200 m.....4. *P. eriantha.*
2. Inflorescences pale to deep yellow to orange, red, rose, pink, or magenta; corollas red, red-purple, orange, or yellow, or white tinged with these colors; calyx lobes 0.3-2.5 (7) mm long; plants of all islands, 0-2200 m.
3. Stipule lobes lanceolate, 4-11 mm long; leaves paired or sometimes ternate; plants of Cuba, 0-1300 m.....7. *P. triphylla.*
3. Stipule lobes triangular, usually very narrowly so, 1-7 (11) mm long; leaves always paired; plants of all islands, 0-2200 m.
4. Corolla tube 18-32 mm long, lobes 4-12 mm long; plants of Jamaica.....
.....6. P. *pulchra.*

4. Corolla tube 7-19 mm long, lobes 1-3.5 mm long; plants of all islands.
   5. Stipule sheaths 1.5-3 mm long; plants found in Greater Antilles, 650-2200 m.....1. *P. alpina.*
   5. Stipule sheaths 0.2-2 mm long; plants of all islands, 0-1300 m.
      6. Corollas yellow; plants of eastern Hispaniola, Puerto Rico, Virgin Island and Lesser Antilles ..... 3. *P. croceoides.*
      6. Corollas dark orange to red or red-purple or white flushed with red-purple; plants of Greater Antilles.
         7. Corolla tube 8-12 mm long; calyx lobes 0.5-2 mm long; plants of all Greater Antilles.....2. *P. crocea.*
         7. Corollas tube 11-16 mm long; calyx lobes 0.3-1 mm long; plants found only in Jamaica.....*8. P. wilesii.*

1. PALICOUREA ALPINA (Swartz) de Candolle

Prodr. 4: 528. 1830. *Psychotria alpina* Swartz, Prodr. 44. 1788. TYPE: Jamaica. Blue Mountains, without date, *O. Swartz s.n.* (Holotype: S, photograph JBSD!). Fig. 2a-c; Little et al., 1974: Fig. 734.

Palicourea brevithyrsa Britton, Bot. Porto Rico 6: 250. 1925. TYPE: Puerto Rico. Mpio. de Adjuntas: Monte Cerrote near Adjuntas, 15 Mar 1915, *Britton & Brown 5427* (Holotype: NY!; Isotypes: F!, MO!, UPR!, US!).

Erect shrubs or small trees to 6 m tall, glabrate to minutely puberulent or hirtellous. *Leaves* paired, the blades (3.5) 8-16.5 cm long, (1.2) 2.5-5.8 cm wide, ca. 2.3-5 times as long as wide, elliptic to somewhat oblong, acute to acuminate at apex with tip 5-10 mm long, cuneate to obtuse at base, chartaceous, both surfaces glabrate but costa and secondary veins hirtellous below and sometimes above as well; secondary veins (7) 10-17 on each side of costa, broadly curved, often looping to interconnect near apex, 1 (3) intersecondary veins usually present between each pair of secondary veins; margins straight; petioles 0.3-2 cm long, vesture similar to that of costa. Stipules forming a continuous sheath, glabrate or hirtellous; sheath 1.5-3 mm long, the lobes 2-7 mm long, very narrowly triangular, acute. *Inflorescences* 3-9 cm long, 2-8 cm broad, ca. 0.6-1.7 times as long as wide at base, pyramidal; bracts 0.5-7 mm long, triangular to narrowly so, acute to rounded, sometimes ciliolate, those subtending primary branches ca. 2-7 mm long, those subtending pedicels ca. 0.5-1.5 mm long, bracteoles and colleters absent; peduncles 1-3.5 cm long, not geniculate at base; pedicels 2-7 mm long, peduncle, axis, branches, bracts, and pedicels red to pink or orange, minutely puberulent to hirtellous or sometimes glabrous, the bracts always glabrous. *Flowers* monomorphic, similar to long-styled form. Calyx green to yellow or orange, minutely puberulous; limb divided for 1/2-3/4 of its length, the lobes 0.5-1.2 mm long, frequently unequal, triangular, acute to rounded. Corolla tubular to weakly infundibular, creamy white to yellow turning orange when old and often becoming flushed with pink or purple, carnose, glabrous or slightly to densely pubescent externally with stout multicellular hairs to 0.5 mm long, glabrous internally except for a ring ca. 1-2 mm wide of pilose vesture at ca. 1/5 the length of the tube above base; tube 11-19 mm long; lobes 1.5-

3 mm long. Anthers 3-4 mm long. Style 11-23 mm long, the stigmatic portion 0.5-1 mm long. Disk 0.5 mm long, annular. *Infructescences* similar in size and proportion to inflorescences, purple or red-purple. *Fruit* 4.5-7 mm long, 4.5-6 mm wide, ovoid to ellipsoid, compressed laterally, glabrate to puberulent; pyrene ridges rounded.

Representative specimens examined: **CUBA.** VILLA CLARA [formerly Las Villas]: Lomas de Siguanea at Río Navarro, *Ekman 13913* (F, S). SANCTI-SPIRITUS [formerly Las Villas]: Buenos Aires, Trinidad Hills, *Jack 5982* (A, US), *7416* (A, F, US), *8061* (A, NY, S, US). GRANMA [formerly Oriente]: near summit of La Bayamesa, crest of Sierra Maestra, *Morton 9367* (BM, F, JBSD). SANTIAGO DE CUBA [formerly Oriente]: Loma del Gato in Sierra Maestra, *Ekman 6953* (F, G, S). GUANTANAMO [formerly Oriente]: southern Baracoa, Puntón del Mate, Sierra de Imias, *León 12172* (NY). **JAMAICA.** SURREY: *St. Andrew*: Mount Horeb, Fairy Glade, *Crosby et al. 376* (F, MO, NY). *Portland*: John Crow Mountains, SW end, ridge from Corn Puss Gap to Crown Peak, *Wilson & Murray 598* (BM, G, S, US). *St. Thomas*: upper western ridge of Blue Mountain Peak, *Maxon 10019* (BM, S, US). **HISPANIOLA. HAITI.** *Sud*: Morne de La Hotte ad Ma Blanche, *Ekman H591* (S). **DOMINICAN REPUBLIC.** *La Vega*: ladera del norte de la Loma de La Sal, frente al Valle de Jarabacoa, 19°05'N, 70°35'Oeste, *Zanoni et al. 36363* (JBSD, UPRRP). *Peravia*: San José de Ocoa, El Manaclar, 18°31'N, 70°27'Oeste, *Mejía 298* (JBSD). **PUERTO RICO.** Adjuntas, Monte Guilarte, *Monachino 747* (SJ); Cerro La Punta, Toro Negro Division, Caribbean National Forest [now Commonwealth Forest], *Little 13681* (BM, GH, NY); Sierra de Juncos, in monte Guvuy [sic; Cubuy], *Sintenis 2686* (BM, G, GH, K, M, P, S, US).

Distribution (Fig. 3). Cuba, Jamaica, Hispaniola, and Puerto Rico, in wet forests and edges, usually on ridges and in cloud forest, 650-2200 m.

Phenology. Collected in flower from January through September and in November, and in fruit from January through April, June through October, and in December.

Palicourea alpina can be separated from all other species of *Palicourea* in the Greater Antilles except *P. eriantha* by the length and comparative development of its stipule sheaths, which are 1.5-3 mm long in contrast to 1 mm long or shorter in the other species found in this region. *Palicourea alpina* is frequently confused with *P. croceoides*, which also has red inflorescence branches and tubular yellow corollas and may have stipule sheaths to 2 mm long in populations in the Lesser Antilles. However, *P. croceoides* has shorter stipule sheats in the Greater Antilles, and corolla tubes 7-13 mm long in contrast to 11-19 mm long in *P. alpina*. *Palicourea croceoides* is also characteristically found at lower elevations than *P. alpina*, 0-1300 m in contrast to 650-2200 m, respectively. *Palicourea* eriantha of Hispaniola is also similar to *P. alpina*. This species has stipules and corolla of similar size, and a similar elevation range. The distinctions between these two species are discussed under the treatment of *P. eriantha*.

There is marked variation in pubescence among individuals of *P. alpina*, from completely glabrous to densely hirtellous along the abaxial leaf midveins and on the outside of the corolla tube. No other characteristics are correlated with this variation, and individuals observed within one population in Puerto Rico vary widely in this

character. A similar range of pubescence is seen in other species, for example *P. eriantha* of Hispaniola and *P. padifolia* (Willdenow) Taylor & Lorence of Central America, and seems to have no taxonomic significance.

Adams (1972) tacitly combined this species with *Palicourea padifolia* (Roemer & Schultes) Taylor & Lorence, a rather weedy distylous species of wet montane Central America. However, these species can be distinguished by the characteristics discussed by Taylor (1989). Based on these morphological differences and their geographic separation, they are maintained here. *Palicourea padifolia* appears to be the mainland species most closely related to *P. alpina*; *P. alpina* and *P. eriantha* appear to be sister groups (Fig. 1).

Palicourea brevithyrsa Britton was separated from *P. alpina* based on its relatively short and dense hirtellous inflorescences. It has been incorrectly cited in synonymy with *P. crocea* by some authors (Little et al., 1974; Liogier & Martorell, 1982), but possesses the relatively well developed stipule sheats, long corollas, and high ridgetop forest habitat characteristic of *P. alpina*. The pubescence does not seem significant, as discussed above, and the inflorescences of adjacent plants vary markedly in size in the area from which the type was collected. Plants inside the forest have inflorescences similar in size and degree of expansion to those of typical *P. alpina*, while those in sunny windy sites have inflorescences of the "P. brevithyrsa" type. Therefore, *P. brevithyrsa* is here combined with *P. alpina*. *Palicourea brevithyrsa* as known from only one population at the type locality has been proposed for consideration as an endangered endemic by the Commonwealth of Puerto Rico (Woodbury et al., 1975), but this does not seem warranted when the species is combined with *P. alpina*, which is known from other mountaintops on the island and form other islands. However, *P. alpina* should be considered rare in Puerto Rico, and is subject to extinction on all islands due to ongoing habitat destruction, even though it multiplies in response to disturbance (Weaver, 1990).

Palicourea alpina was reported from Guadeloupe and Dominica by Little et al. (1974), and from Guadeloupe by Fournet (1978). No specimens have been seen. This species was not listed by Howard (1989) from any of the Lesser Antilles, and was specifically excluded from the flora of Dominica by Nicolson (1991). The report probably was based on Grisebach's (1857) mention of a *Palicourea* species that fits the description of *P. alpina* growing in Guadeloupe. He referred this to *P. mexicanum* Bentham, a synonym of *P. padifolia*. Grisebach later (1861) repeated this report using the older name *P. alpina*. This was based on a collection by Imray, which has not been seen. These reports may have been based on misidentifications of specimens of *P. croceoides*, although it is also possible that *P. alpina* was present on the mountaintops of these islands and has subsequently disappeared, perhaps due to forest destruction and volcanic activity.

In Puerto Rico, *P. alpina* is markedly seasonal in flowering and leaf flushing, in contrast to most other West Indian *Palicourea* species. A few flowering individuals may be found at most times of the year, but most plants flower from late April to early July, and virtually no flowering plants can be found in January and early February. The

seasons are not well marked in Puerto Rico, but January and February are generally the dryest months while October and November are the wettest (Colón, 1989; Ewel & Whitmore, 1973).

Called cafetán (Dominican Republic, reported as "tafetán" by Moscoso, 1943, apparently a misspelling, and Puerto Rico, Little et al., 1974), cenizoso cimarrón (Puerto Rico, Little et al., 1974), tapa camino (Cuba, Little et al., 1974), and bois cabrit montagne (Guadeloupe, Little et al., 1974).

2. PALICOUREA CROCEA (Swartz) Roemer & Schultes
Syst. Veg. 5: 193. 1819. *Psychotria crocea* Swartz, Prodr. 44. 1788. *Uragoga crocea* (Swartz) Kuntze, Revis. gen. pl. 1: 299. 1891. TYPE: Jamaica. Without location, without date, *O. Swartz s. n.* (Holotype: S!, photograph JBSD!). Taylor, 1989: Fig. 5g, h.

Palicourea coccinea Poiteau ex de Candolle, Prodr. 4: 529. 1830. SYNTYPES: Dominican Republic. Without location, without date, *P.A. Poiteau s. n.* (P!). Puerto Rico. Without location, without date, *C.G.L. Bertero s. n.* [G-DC, photograph (Rockefeller neg. #33544) F!, MO!].

Palicourea crocea α tenuifolia Grisebach, Fl. Brit. W. I. 345. 1864. TYPE: not designated.

Erect shrubs 1-2 m tall, glabrous to minutely puberulous. *Leaves* paired, the blades 6-18.5 cm long, 2.2-7 cm wide, ca. 1.9-3.4 times as long as wide, elliptic to slightly ovate, obovate, or oblong, acute to acuminate at apex with the tip to 1 cm long, acute to sometimes attenuate at base, chartaceous, glabrous to minutely pustulose to puberulous, often hirtellous abaxially along costa; secondary veins 9-15 (18) on each side of costa, broadly curved, with 1 (3) intersecondary veins usually present between each pair of secondary veins; margins straight; petioles 1-12 mm long, vesture similar to that of costa. Stipules forming a continuous sheath, glabrate to minutely puberulous; sheat 0.2-1 mm long, the lobes 1-4 mm long, very narrowly triangular, acute. *Inflorescences* 2.5-15 cm long, 1.5-10 cm broad, ca. 1-2 times as long as broad at base, pyramidal; bracts 0.5-20 mm long, triangular to narrowly so or ligulate, acute to obtusely rounded, sometimes ciliolate, those subtending primary branches ca. 2-20 mm long, those subtending pedicels ca. 0.5-2 mm long, bracteoles often present, to 2 mm long, shorter than bracts, colleters absent; peduncles 1.5-23.5 cm long, not geniculate at base; pedicels 2-11 mm long; peduncle, axis, branches, and bracts orange to red with the pedicels usually flushed with yellow, glabrous to minutely puberulous. *Flowers* distylous. Calyx green on ovary portion, yellow to orange on limb, glabrous to minutely puberulous; limb divided nearly to base, the lobes 0.5-2 mm long, frequently unequal, triangular to ligulate, acute to rounded. Corolla tubular, dark orange to deep red, somewhat carnose, glabrous or sparsely to moderately hirtellous externally, glabrous internally except for a ring of pilose vesture ca. 0.5-1 mm wide at ca. 1/4-1/3 the length of the tube above base; tube 8-12 mm long; lobes 1-2.5 mm long. Anthers in both long- and short- styled forms 2.2-2.5 mm long. Style in long form 5.5-10 mm long, the stigmatic portion 0.5-1.5 mm long, in short form 4-5 mm long, the stigmatic portion

2 mm long. Disk 0.8-1 mm high, annular. *Infructescences* similar in size to inflorescence, often proportionately wider, purple. Fruit 3-4.5 mm long, 3.5-4.5 mm wide, ellipsoid to slightly ovoid, compressed laterally, glabrate to puberulent; pyrene ridges rounded.

Representative specimens examined. **CUBA.** PINAR DEL RIO: vicinity of Los Palacios, *Shafer 11802* (F, JBSD, MO, NY, US). ISLA DE LA JUVENTUD [ISLE OF PINES]: vicinity of San Pedro, *Britton et al. 14463* (F, GH, NY, US). VILLA CLARA [formerly Las Villas]: Santa Clara, Gavilaucito, Banao Mountains, *León & Roca 8448* (NY). GRANMA [formerly Oriente]: Bayotte, prope Río Canto, *Ekman 6194* (F, G, MO, S). **JAMAICA.** CORNWALL: *Hanover*: Askenish, *Proctor 10008* (US). *St. Elizabeth:* Magotty, *Orcutt 2070* (BM). *Trelawney*: Oxford, near Troy, *Harris 9435* (F, NY, US). MIDDLESEX: *St. Ann*: Williamsfield property (Alumina Jamaica area to be mined in 1958), 0.75 mi due NE of Faith's Pen post office, *Howard & Proctor 14991* (A, BM). *St. Catherine*: Charlton Pond near Ewarton, *Crosby et al. 391* (DUKE, F, MO, NY). SURREY: *St. Andrew*: between Stoney Hill and Río Pedro, *Philipson 645* (A, BM). *Portland*: Rodney Hall, *Adams 9284* (BM, DUKE). *St. Thomas*: Bowden Pen, *Crosby & Anderson 1073* (DUKE, F, NY). **HISPANIOLA. HAITI.** *Nord*: Bayeux, on road to Bornes, *Ekman H2618* (G, GH, K, S, US). *L'Artibonité*: Kalacroix, sector Dessalines, *Leonard 7836* (NY, US). *Sud*: Miragoane and vicinity, Bellevue, *Eyerdam 457* (F, GH, NY, US). **DOMINICAN REPUBLIC.** *Santiago*: Sierra de Yaroa, Votava & Liogier 7 (NY). *Barahona*: prope Paradis, *Fuertes 335* (A, BM, F, G, GH, K, MO, NY, P, S, US). *La Vega*: La Manaclita, 10 miles S of La Vega, *Liogier 15838* (GH, NY, P). *Sánchez Ramírez*: Maimón, Campamento Los Pinos, *Liogier & Liogier 26663* (JBSD, NY, UPR). *San Cristóbal*: Río Comate at Sierra de Agua, 18°50.5'N, 69°35'W, *Mejía & Zanoni 8035* (JBSD). *Monte Plata*: Bayaguana, *Liogier 19003* (JBSD, NY). *Distrito Nacional*: *Ekman H11067* (A, NY, S). *Samaná*: Sánchez, *Rose et al. 4325* (NY, P, US). *El Seibo*: 14 km. E of Sabana de la Mar, on road to Miches, 19°01'N, 69°16.5'W, *Mejía et al.* 10149 (MO, NY). *La Altagracia*: próximo al nacimiento del Río Llano, Km. 22 de Santana a La Colorada, NO de Higüey, 19°46'N, 68°17'W, *Mejía & Ramírez 11119* (JBSD, NY). **PUERTO RICO.** La Chicita [sic; Chiquita] near Maricao, *Britton & Cowell 4264* (F, NY, SJ, US); Cerro de la Pandura, *Eggers 400* (G, GH, P), *460* (G, P).

Distribution (Fig. 4). Southern Mexico, Greater Antilles, and Central America to southern Brazil and Paraguay. Cuba, Jamaica, Hispaniola, and Puerto Rico, in moist to wet forest and thickets, usually in shaded sites, 0-800 m.

Phenology. Flowering and fruiting throughout the year.

Palicourea crocea can be recognized by its relatively short stipule sheaths 0.2 to 1 mm long and deep orange to dark red corollas borne on usually yellow pedicels. It is similar to *P. croceoides*, and has been frequently confused and combined with that species (Adams, 1972; Grisebach, 1861; Steyermark, 1972, 1974; Little et al., 1974; Liogier & Martorell, 1982; Howard, 1989; Nicolson, 1991). *Palicourea croceoides* can be distinguished from *P. crocea* by its yellow corollas with lobes 1.5 to 3.5 mm long borne on red to orange pedicels, in contrast to 1 to 2.5 mm long on orange to usually yellow

pedicels in *P. crocea*, and its pyrenes with angled ribs in contrast to rounded ribs in *P. crocea*. These two species are sympatric only in Puerto Rico and eastern Hispaniola, where they may be found growing in mixed populations. They have been regarded as two color forms of one species by some authors, or more commonly the difference in color has not been noted. However, the reversed corolla and pedicel colors are consistently correlated with corolla lobe length and pyrene characters, and preliminary data suggest a consistent difference in ploidy between them as well (M. Kiehn, pers. comm.). Plants of *P. crocea* are usually smaller than those of *P. croceoides*, about 1 m or shorter in contrast to 1.5 m or taller, respectively. The inflorescences of *P. crocea* generally have fewer total flowers but more flowers open at one time (3 to 5) than *P. croceoides* (1 to 2). The plant illustrated by Little et al. (1974; Fig. 736) as *P. crocea* is actually *P. croceoides*.

Palicourea crocea is distylous throughout its range in the Antilles as well as in mainland populations. It appears to be most closely related to several other species of *Palicourea* from the Amazon basin, notably *P. longiflora* (Aublet) A. Richard and *P. marcgravii* St. Hilaire (Fig. 1). These South American species appear to be related also to *P. croceoides*, although the two Antillean species may not be sister groups.

Called cachimbo (Puerto Rico, Liogier & Martorell, 1982), tapa camino, ponasí (Cuba, Little et al., 1974), cafecillo (Dominican Republic, Jiménez in herb.).

3. PALICOUREA CROCEOIDES W. Hamilton

Prodr. pl. Ind. occid. 29. 1825. TYPE: Antilles. Without location, without date, *W. Hamilton s. n.* (Holotype: P!, microfiche!). Little et al., 1974: Figs. 736, 738; Howard, 1989: Fig. 194.

Palicourea riparia Bentham, J. Bot. (Hooker) 3: 224. 1841. *Palicourea crocea* α *riparia* (Bentham) Grisebach, Fl. Brit. W. I. 345. 1864. *Uragoga riparia* (Bentham) O. Kuntze, Revis. gen. pl. 2: 962. 1891. TYPE: Guayana. Banks of rivers, *Schomburgk 337* (Holotype: K!, photograph NY!; Isotypes: GH!, NY!, P!).

Palicourea martinicensis Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 11: 230. 1936. TYPE: Martinique. Piton de l'Alba, Mar. 1869, *L. Hahn 802* (Holotype: P!; Isotypes: F!, K!).

Erect shrubs to small trees, to 3 (5) m tall, glabrous to puberulous or hirtellous, *Leaves* paired, the blades 4.5-24 cm long, 1.5-9 cm wide, ca. 2.1-4.6 times as long as wide, elliptic to somewhat oblong or ovate, acute to acuminate at apex with the tip to 25 mm long, cuneate to obtuse at base, chartaceous, glabrous or often pustulose or puberulous adaxially or on both surfaces, usually with a line of pilosulous pubescence abaxially along juncture of blade and costa; secondary veins 5-12 (16) on each side of costa, straight to curved, 1 (3) intersecondary veins usually present between each pair of secondary veins; margins straight; petioles 2-30 mm long, vesture similar to that of costa. Stipules forming a continuous sheath, glabrous to puberulous; sheath (0.2) 0.5-2 mm long, the lobes 1-6 (11) mm long, triangular to very narrowly so, acute. *Inflorescences* 1.5-11 cm long, 2-12.5 cm wide, ca. 0.6-1.5 times as long as broad,

pyramidal to somewhat corymbi-form; bracts 0.5-20 mm long, triangular to narrowly so or ligulate, acute to obtusely rounded, sometimes ciliolate, those subtending primary branches ca. 1-20 mm long, those subtending pedicels ca. 0.5-1.5 mm long, bracteoles often present also, to 2 mm long, shorter than bracts and usually triangular, colleters absent; peduncles 2-12 cm long, not geniculate at base; pedicels (0) 1-12 mm long; peduncle, axis, branches, bracts, and pedicels bright red, glabrous or more usually puberulous to hirtellous. *Flowers* distylous. Calyx red to orange, glabrous to minutely puberulous; limb divided for 3/4 to nearly all of its length, the lobes 0.5-2.5 (7) mm long, frequently strongly unequal, triangular to ligulate, acute to rounded. Corolla tubular to somewhat infundibular, bright yellow, somewhat carnose, glabrous or hirtellous externally, glabrous internally except for a dense ring of pilose vesture ca. 0.5-1 mm wide at ca. 1/3-1/4 the length of the tube above base; tube 7-13 mm long; lobes 1.5-3.5 mm long. Anthers in both long -and short- styled form 2.5-4 mm long. Style in long form 8-14 mm long with stigmatic portion ca. 0.5-1 mm long, in short form 4-7 mm long with stigmatic portion ca. 2-3.2 mm long. Disk 0.8-1.5 mm long, annular. Infructescences similar in size to *inflorescences*, usually proportionately somewhat wider, red-purple. *Fruit* 4-6 mm long, 4.5-6 mm wide, ovoid, compressed laterally, glabrate to puberulent; pyrene ridges angled.

Representative specimens examined. **HISPANIOLA.** *DOMINICAN REPUBLIC. Samaná*: N of Pan de Azúcar, *Ekman H15092* (G, GH, K, NY, S, US). **PUERTO RICO.** Río Piedras, *Little 14902* (BM, GH, NY); 7 mi S of Caguas, *Heller & Heller 274* (F, K, NY). **ST. JOHN.** Bordeaux Mountain, *Mori et al. 17039* (BM). **ST. CROIX.** Without location, without date, *Vahlsen s. n.* (S). **TORTOLA.** High Bush, *Britton & Shafer 820* (K, NY, US). **ST. BARTHELEMY.** Without location, without date, Forsstrom s. n. (S). **ST. KITTS.** Near Sandy Point, *Britton & Colwell 112* (NY, US). **NEVIS.** Nevis Peak, S slope, *Smith 10502* (NY, S, US), 10543 (K, NY, S, US). **ANTIGUA.** Macarthy Valley, in southwest district, *Box 1059* (BM, F, NY, US). **MONTSERRAT.** Chances Mountain, at Chances Pond, *Howard 11888* (A, BM). **GUADELOUPE.** Baines-jaunes, *Funck & Schlim 65* (F, G, P). **DOMINICA.** Slopes of Micotrin along trail 0.5 mi beyond Laudet to 0.5 mi beyond Freshwater Lake, *Wilbur et al. 7433* (F, GH, MO). **MARTINIQUE.** Camp de l'Alma, Pitons du Carbet, *Duss 602* (F, MO, NY, US). **ST. LUCIA.** Castries, along Dennery Road, *Howard 11295* (BM, GH, NY). **GRENADA.** St. David, Minorca Estate above Windsor Forest, *Proctor 16906* (A, BM).

Distribution (Fig. 5). Antilles to Amazonian Brazil: northeastern Hispaniola, Puerto Rico, and the Lesser Antilles, in moist to wet forest, thickets, and edges, 0-1300 m.

Phenology. Flowering and fruiting throughout the year.

Palicourea croceoides can be recognized by its bright red inflorescence branches and yellow corollas, and its stipules with very short sheaths 0.2 to 1 mm long and usually relatively long triangular lobes 1 to 11 mm long. Only *P. alpina* has a similar color pattern; the separation of these species is discussed in the treatment of that species. *Palicourea croceoides* has frequently been confused and combined with *P. crocea*; the distinctions between these are discussed under the treatment of the latter species.

Palicourea croceoides is conspicuous and common in secondary growth, and is the most frequently collected species of *Palicourea* in the Antilles.

The epithet "*croceoides*" has been passed over by previous authors as being of questionable application (Howard et al., 1981), or treated as a synonym of *P. crocea* (Howard, 1989). Hamilton had field experience in the Antilles, and stated clearly in his description that this species is similar to *P. crocea* but distinguished by its yellow corollas, and that it is found in the Lesser Antilles. These characters accurately and completely separate *P. croceoides* from all other Antillean *Palicourea* species. A specimen at P designated anonymously as the type of this name clearly represents the Lesser Antillean plants. Although Hamilton credited Desvaux with authorship of the epithet, more recent workers suggest that such names should be credited to Hamilton alone (Howard et al., 1981).

Standley separated *Palicourea martinicensis* based on its relatively long calyx lobes, to 7 mm long, well outside the normal range for *P. croceoides*. These long calyx lobes are found on the type collection and on a few other specimens, *Stehlé 2376* (P!), *Stehlé & Stehlé 2642* (P!), and *Stehlé & Stehlé 4652* (US!). However, Standley's paratype collection, *Hahn 198* (F!, P!), is mixed: the material at F matches that of the type collection, while the material at P has calyx lobes about 1 mm long, similar to typical *P. croceoides*, and is mixed with *Psychotria berteriana* de Candolle, a fact that was not noted by Standley in his annotation or publication of the name. Both sheets were annotated as *Palicourea martinicensis* by Standley. Other collections from the type locality and all other collections from Martinique have calyx lobes about 1 mm long. It seems likely that these three collections represent no more than an unusual local variant in calyx lobe length. Therefore, P. *martinicensis* is here combined with *P. croceoides*.

Palicourea croceoides is distylous throughout its range in the Antilles as well as in mainland populations. It appears to be most closely related to several other *Palicourea* species found in the Amazon basin, notably *P. longiflora* (Aublet) A. Richard and *P. marcgravii* St. Hilaire (Fig. 1). These South American species appear to be related also to *P. crocea*, although the two Antillean species may not be sister groups.

Palicourea croceoides was the first plant to colonize an area experimentally burned with radiation in Puerto Rico (Odum & Pigeon, 1970), and it regenerated, flowered, and fruited rapidly in hurricane-damage forests in eastern Puerto Rico in 1989 (see the introductory section on Reproductive Biology). The ecological physiology of this plant in Puerto Rico was studied by LeBrón (1979), the effect of radiation on its cytology by Venator & Koo (1970), and the reproduction and genetic variability of populations by Melampy (unpub.).

Called palo de cachimbo (Puerto Rico, Little et al., 1974), yellow-cedar (Tortola, Little et al., 1974), bois puce (St. Lucia, Little et al., 1974), bois de l'encre, bois cabrit, bois fou-fou (Martinique, Little et al., 1974), bois cabrit noir, bois fou-fou, arbre a l'encre (Guadeloupe, Cabre & Tanon, 1939); and reputed to be used as an emetic in Guadeloupe (Cabre & Tanon, 1939).

4. PALICOUREA ERIANTHA de Candolle

Prodr. 4: 528. 1830. *Palicourea alpina* var. *eriantha* (de Candolle) Grisebach,

Cat. Cub. 138. 1866. TYPE: Dominican Republic. Without location, without date, without collector or number (Holotype: G-DC, microfiche!.) Fig. 2d.

Erect shrubs or small trees to 6.5 m tall, glabrate to hirtellous. *Leaves* paired, the blades 8-13.5 cm long, 2.5-4.5 cm wide, about 2.9-3.6 times as long as wide, elliptic, acute to acuminate at apex with the tip ca. 5 mm long, cuneate to obtuse at base, chartaceous, both surfaces glabrate or the abaxial sometimes hirtellous, costa and often also secondary veins hirtellous below and sometimes also above as well; secondary veins 11-14 on each side of costa, broadly curved, often looping to interconnect near apex, 1 (3) intersecondary veins usually present between each pair of secondary veins; margins straight; petioles 3-20 mm long, vesture similar to that of costa. Stipules forming a continuous sheath, glabrate to hirtellous; sheath 2-3 mm long, the lobes 2-3 mm long, narrowly triangular, acute. *Inflorescences* 6-10.5 cm long, 4.5-9 cm broad, ca. 0.8-1.3 times as long as broad at the base, pyramidal; bracts 1-5 mm long, triangular to narrowly so, acute to obtusely rounded, sometimes ciliate, those subtending primary branches ca. 3-5 mm long, those subtending pedicels ca. 1-1.5 mm long; bracteoles and colleters absent; peduncles 2.5-4.5 cm long, not geniculate at base; pedicels 2-7 mm long; peduncle, axis, branches, bracts, and pedicels blue to violet, minutely pilosulous to hirtellous or sometimes glabrate, the bracts usually glabrous. *Flowers* monomorphic, similar to long-styled form. Calyx purple to blue, glabrous to minutely pilosulous; limb divided for 1/2-3/4 of its length, the lobes 1-3.5 mm long, usually strongly unequal, triangular to ligulate or lanceolate, acute to somewhat rounded, sometimes ciliolate. Corolla tubular, blue, carnose, glabrous of slightly to densely pubescent externally with stout multicellular hairs to 0.5 mm long, glabrous internally except for a ring ca. 1-2 mm wide of pilose vesture at ca. 1/5 the length of corolla tube above base; tube 12-20 mm long; lobes 1.5-4 mm long. Anthers 3-4 mm long. Style 13-21 mm long, the stigmatic portion 0.5-2 mm long. Disk 0.5 mm high, annular. *Infructescences* similar in size, color, and proportion to inflorescences. *Fruit* 4.5-6 mm long, 4.5-5.5 mm wide, ovoid to ellipsoid, compressed laterally, glabrate to puberulent; pyrene ridges rounded.

Representative specimens examined: **HISPANIOLA. HAITI.** *Sud*: Massif de La Hotte, western group, Torbec, above La Mare-Proux, *Ekman H5306* (GH, S). *Ouest*: Massif de La Selle, Marne Calabi, *Ekman H1561* (A, K, G, GH, NY, S). **DOMINICAN REPUBLIC.** *Monte Cristi*: Cordillera Central, Monción, Lagunas de Cenobí, *Ekman H12863* (GH, S). *San Juan*: Piedra del Aguacate to Río del Oro, *Howard & Howard 9364* (BM, F, GH, NY, S). *Independencia*: entre Cerros de Plan Ciquen y Loma El Hoyazo, 35 km de La Descubierta, *Zanoni et al. 24892* (JBSD). Barahona: Morne La Jó, *Zanoni & García 30365* (JBSD). *Pedernales*: Las Mercedes, *Jiménez 4501* (US). *Santiago*: distrito de San José, arriba de Loma Bajita, *Valeur 1020* (MO, NY). *Azua*: arriba de la loma Arroyo Hondo, entre Sabana de Miguel Martín y El Cercado, 18°38'N, 70°43'Oeste, *Zanoni & Pimentel 22186* (JBSD, MO, UPRRP). *La Vega*: prope Constanza, *von Tuerckheim 2990* (A, BM, G, GH, K, MO, NY, S), *3318* (A, BM, G, GH, K, M, MO, P, NY, S). *Peravia*: La Nevera, 25 km N of Los Arroyos de Ocoa, 18°36.5'N, 70°35.5'Oeste, *Mejía & Zanoni 8702* (JBSD).

Phenology. Collected in flower from May through November, in fruit in January, March, May, July, August, and December.

Distribution (Fig. 3). Hispaniola, in both broadleaf and wet pine forests, 700-2200 m.

Palicourea eriantha can be recognized by its blue to purple inflorescences, blue corollas, and relatively long calyx lobes, 1 to 3.5 mm long. In the Antilles only *Psychotria toensis* Britton & Wilson of western Cuba also has blue flowers. This latter species lacks the ring of trichomes inside the corollas and has its sessile flowers arranged in closely set glomerules, in contrast to the pedicellate flowers in open inflorescences of *P. eriantha*. *Palicourea alpina* is similar to *P. eriantha*, but has cream to yelow, orange, or salmon-pink corollas borne on red to orange inflorescences branches and calyx lobes 0.5 to 1.2 mm long. These species are sympatric, and are not always easily separated when corolla color is not noted or when the specimen is in fruit. Relatively long calyx lobes, to 2.5 mm long, can also be found in some plants of *P. croceoides* from Hispaniola, but this last species can be recognized by its reduced stipule sheath, 0.5 to 2 mm long in contrast to 2 to 3 mm long in *P. eriantha*, and its yellow corollas borne on red inflorescence branches.

Palicourea eriantha was originally separated from *P. alpina* based on its densely pubescent corollas. However, glabrous and densely pubescent corollas are found on adjacent plants of both species, and this character appears to have no taxonomic significance. More recently, the blue corollas and inflorescence branches have been overlooked and *P. eriantha* has been combined with *P. alpina* (Grisebach, 1864, 1866; Moscoso, 1943; Urban, 1921). Inflorescence and corolla colors are important species-level characteristics (Taylor, 1989), and combined with the difference in calyx lobe length they support the separation of *P. eriantha* and *P. alpina*.

Palicourea alpina and *P. eriantha* appear to be sister groups; they appear to be most closely related to *P. padifolia* of Central America (Fig. 1).

Called cafetán (Dominican Republic, reported as "tafetán" by Moscoso, 1945, apparently a misspelling).

5. PALICOUREA GUIANENSIS Aublet

Hist. pl. Guiane 1: 173, t. 66. 1775. *Psychotria palicourea* Swartz, Fl. Ind. Occ. 433. 1797, illegitimate name (superfluous). *Stephanium guianense* (Aublet) Raeuschel, Nomencl. bot. 56. 1797. *Simira palicourea* (Swartz) Poiret, Encycl. 7: 196. 1804. *Uragoga palicourea* (Swartz) O. Kuntze, Revis. gen. pl. 2: 300, 983. 1891. TYPE: French Guiana. Caux, without date, *F. Aublet s. n.* (Holotype: BM!). Taylor, 1989: Fig. 20d, f; Little et al., 1974: Fig. 735.

Palicourea barbinervia de Candolle, Prodr. 4: 530. 1830. *Palicourea guianensis* subsp. *barbinervia* (de Candolle) Steyermark, Mem. New York Bot. Gard. 23: 730. 1972. TYPE: Dominican Republic. Without location, without date, *C.G.L. Bertero s. n.* [Holotype: G-DC, photographs (Rockefeller neg. #33545) F!, MO!].

Psychotria lutea Sprengel ex de Candolle, Prodr. 4: 530. 1830, illegitimate name (presented as synonym).

Erect shrubs or small trees to 8 m tall, glabrous or minutely puberulent. *Leaves* paired, the blades 13-25 (37) cm long, 5-13 (24) cm wide, ca. 1.8-2.8 times as long as wide, elliptic to somewhat ovate or oblong, acute to acuminate at apex with the tip 5-10 mm long, cuneate, at base, membranaceous to chartaceous, both surfaces glabrate or minutely puberulent or sometimes slightly pustulose, frequently the costa and less often also the secondary veins hispidulous to pilosulous along their juncture with the lamina; secondary veins 12-16 (18) on each side of the costa, broadly curved, 1(-2) intersecondary veins usually present between each pair of secondary veins; margins straight; petioles 0.6-2 (3.5) cm long, vesture similar to that of costa. Stipules forming a continuous sheath, glabrous or occassionally minutely puberulent; sheath 0.5-1 mm long, the lobes 4-6.5 mm long, elliptic to ligulate, rounded, ciliolate. *Inflorescences* 8-14 cm long, 5-19 cm broad, ca. 0.7-1.3 times as long as broad at the base , pyramidal; bracts 0.5-6 mm long, triangular, acute, entire or ciliolate, those subtending primary branches ca. 2-6 mm long, those subtending pedicels ca. 0.5-1 mm long, bracteoles and colleters absent; peduncles 5-11 cm long, not geniculate at base; pedicels 1-8 mm long; peduncle, axis, branches, bracts, and pedicels yellow, glabrous, or usually minutely puberulous or hispidulous. *Flowers* monomorphic, similar to long-styled form. Calyx green to yellow, glabrous or minutely puberulous; limb divided to base, the lobes 0.25-0.6 mm long, usually equal, triangular, acute to rounded, often ciliolate. Corolla tubular to weakly infundibuliform, red, pink, yellow, or cream, somewhat membranaceous, puberulent externally with stout multicellular trichomes and appearing tomentulous or farinaceous, glabrous internally except for a ring about 1-2 mm wide of pilose vesture at ca. 1/5 the length of the corolla tube above the base; tube 9-12 mm long; lobes 1-2 mm long. Anthers 3-3.5 mm long. Styles 10-13 mm long, the stigmatic portion 0.5-1 mm long. Disk 0.5-1 mm high, annular. *Infructescences* similar in size to inflorescences, usually proportionately broader, purple or red-purple. *Fruit* 3-4.5 mm long and wide, ovoid to ellipsoid, compressed laterally, glabrous or minutely and sparsely puberulous; pyrene ridges rounded.

Additional specimens examined. **CUBA.** Without province, Santa Ana, *Eggers 5032* (A, K, P, US); entre Los Mulos and La Corea, camino de Ulayan abajo a Sierra Cristal, *López Esquinal 209* (US). HOLGUIN [formerly Oriente]: Monte La Plancha, Sierra de Nipe, *Carabia 3672* (NY); Plancha trail, Mesura to Woodfred, Shafer 3888 (F, NY, US). SANTIAGO DE CUBA [formerly Oriente]: northern spur of the Sierra Maestra, W of Río Yao, *Morton & Acuña 3449* (JBSD, US); upper Río Navas, *Shafer 4378* (A, F, NY, US). GUANTANAMO [formerly Oriente]: Monte Centeno, Oca, *Acuña 13367* (F); prope Baracoa, inter Santa María et Jiguani prope Iberia ad Taco Bay, *Ekman 3773a* (F, S), *3773b* (S); Sierra de Cristal prope Río Lebisa in manacales, *Ekman 6853* (G, S); at headwaters of Río Lebisa, *Ekman 15938* (F, S); La Prenda Guantánamo, *Hioram s. n.* [28 Dec 1919] (NY), *4232* (GH, NY, US); Baracoa, *Underwood & Earle* 1402 (NY). **JAMAICA.** SURREY: *Portland*: near Moore Town, *Mitchell 10071* (BM, F, K, NY, P, US); Rodney Hall district, between Windsor Forest and Islington, *Proctor 22091* (A, NY); 1 mi SE of Millbank, *Proctor 31069* (F, MO); Rodney Hall, *Adams 9071* (BM). **HISPANIOLA. HAITI.** *L'Artibonité-Nord Border Region*: Massif du Nord,

Morne Organise, *Ekman H6233* (GH, S, US); Massif du Nord, Valliére, hills N of town, *Ekman H9944* (G, K, S, US). Sud: Massif de La Hotte, western group Jérémie, Source-Cahaouane, *Ekman H10236* (NY). **DOMINICAN REPUBLIC.** Without location, *Wright et al. 210* (F, GH, NY, US), *293* (F, US). *Monte Cristi*: district of Sabaneta, Río Cidra, *Valeur 524* (F, G, K, MO, NY, US). *Santiago*: Cordillera Central; La Cumbre, *Ekman H11556* (G, GH, US). *La Vega*: Los Plátanos, Loma Campana, *Allard 18261* (S, US), *18297* (US), *18298* (US); NE del Río Yuna, *Zanoni et al. 12831* (JBSD). *Duarte*: vicinity of San Francisco de Macorís, Quita Espuela, *Abbott 2156* (GH, US). *Monseñor Nouel-Peravia Border Region*: cabezadas de Río Yuna, Rancho Arriba, Liogier & Liogier 25519 (GH, JBSD, NY). *Samaná*: Samaná Peninsula, vicinity of Laguna, *Abbott 316* (US); prope Sánchez, von *Tuerckheim 3743* (G, K, NY; mixed with *P. crocea*). *El Seibo*: La Mina, sector El Jovero, Miches, *Jiménez & Ariza Julia 5804* (NY); 14 km N of Pedro Sánchez, 18°55'N, 69°07'W, *Terborgh 256* (GH). **PUERTO RICO.** Without location, without date, *Plée 449* (F, P), *L.C. Richard s. n.* (P), *Riedlé s. n.* (F, P), *92* (P), *219* (P); prope Isabela, *Stahl 724* (GH, US); Lares, ad Arones, *Sintenis 5944* (BM, K, MO, P, NY); Maricao, without date , *Cedo A. s. n.* (MAPR); Maricao, *Sintenis 279* (G, GH, P, S, US); 3 mi W of Utuado, near Santa Rosa, *Little & Woodbury 26173* (BM, NY); Utuado, Los Angeles, *Sintenis 6202* (BM, F, G, NY); Toro Negro, rte 149, N of Juana Díaz falls, *Woodbury s. n.* [20 Feb 1961] (NY); Florida, rte 946, km. 3.8, *Woodbury s. n.* [13 Feb 1960] (NY, US); Guavate, *Woodbury s. n.* [15 Aug 1962] (NY); Guavate, *Liogier et al. 29801* (NY); Carite, *Little & Woodbury 25725* (BM, DUKE, NY); Carite, *Wagner 1248* (A, BM, DUKE, MO, WIS). **GRENADA.** Belvidere, *Hunnewell 19538* (GH).

Phenology. Collected in flower January through April, in June, and August through December, and in fruit from January through April, and in June, August, and November.

Distribution (Fig. 6). Southern Mexico and Antilles to southern Brazil and Bolivia. Greater Antilles and Grenada, in moist to wet forests and thickets, 0-1000 (1450) m.

Palicourea guianensis can be separated from other Antillean species of *Palicourea* by its rounded stipule lobes and reatively large leaves, about 5-13 (-24) cm wide compared to 2-9 cm wide in the other species.

The Antillean members of this species have been separated from the continental plants by some authors as *Palicourea barbinervia* de Candolle or *P. guianensis* var. *barbinervia* (de Candolle) Steyermark, but there seems no basis for this. The only character that separates these taxa is the presence of barbate hairs in the axils of the secondary leaf veins. These hairs probably represent domatia. They are present on some plants from continental South America, and absent on some Antillean individuals. The island plants are sometimes weedy but usually produce flowers only as scattered subcanopy trees in wet forests, in contrast to the mainland plants, which flower both as understory trees and as common weedy shrubs in disturbed sites such as roadsides and riverbanks. The Puerto Rican plants show strong seasonality in flowering, fruiting, and flushing of new leaves, whereas mainland Costa Rican plants generally do not. These differences are comparable to ecological variations noted between mainland and island

populations of another species, and do not seem a sufficient basis on which to separate a species or variety with no morphological distinctions.

Some plants of *Palicourea guianensis* from South American have three- or four-celled ovaries (Bremekamp, 1934; Steyermark, 1972), but all specimens seen from the Antilles have bilocular ovaries. Although *Palicourea guianensis* from mainland South America is distylous, only the long-styled form is represent in the Antilles and Central America (Taylor, 1989). The implications of this are discussed in the introductory sections Colonization of the Antilles.

Palicourea guianensis appears to be most closely related to several other species of *Palicourea* found in the Amazon basin, particularly *P. grandifolia* (Roemer & Schultes) Standley and P. buntingii Steyermark.

Called bálsamo real (Puerto Rico, Liogier & Martorell, 1982), cafetán (Puerto Rico, reported as "tafetán" by Little et al., 1974, probably a misspelling based on Moscoso's report), flor de soldado, bleo cimarrón (Cuba, Little et al., 1974), ahoguey blanco, cafetán (Dominican Republic, reported as "tafetán" Little et al., 1974, probably a misspelling).

6. PALICOUREA PULCHRA Grisebach

Fl. Brit. W. I. 345. 1881. TYPE: Jamaica. Without location, without date, Marsh 1814 (Holotype: K!; Isotype: K!). Fig. 7.

Palicourea pulchra var. *hispidula* Proctor, J. Arnold Arbor. 63: 3. 1982. TYPE: Jamaica. Cornwall: Trelawny: Mango Tree Hill, along trail up, 27 May 1967, *Read 1904* (Holotype: US!; Isotypes: A!, MO!, NY!).

Erect shrubs or small trees to 3.5 m tall, glabrous or minutely puberulous to hispidulous. *Leaves* paired, the blades 5.5-15 cm long, 1.5-6.5 cm wide, ca. 1.9-4 times as long as wide, elliptic to lace-elliptic or sometimes oblong, acute to acuminate at apex with the tip 5-10 mm long, acute to cuneate or occasionally obtuse at base, chartaceous to subcoriaceous, usually minutely pustulose, glabrous or occasionally minutely puberulous above and below; secondary veins 7-13 on each side of costa, broadly curved, 1 (2) intersecondary veins usually present between each pair of secondary veins; margins straight; petioles 3-15 mm long, vesture similar to that of costa. Stipules forming a continuous sheath, glabrous or minutely puberulous; sheath 0.3-1 mm long, the lobes 1-4 mm long, very narrowly triangular, acute. *Inflorescences* 2.5-11.5 cm long, 1.5-13 cm broad, ca. 0.6-1.8 times as long as broad at base, pyramidal; bracts 0.3-4.5 mm long, triangular, acute to rounded, sometimes ciliate, those subtending primary branches ca. 0.5-4.5 mm long, those subtending pedicels ca. 0.3-1 mm long; bracteoles and colleters absent; peduncles 2-12 cm long, not geniculate at base; pedicels 1-11 mm long; peduncle, axis, branches, bracts, and pedicels red-purple, glabrous or minutely puberulous. *Flowers* monomorphic. Calyx red-purple, glabrous or minutely puberulous; limb divided for 2/3 to nearly all of its length, the lobes 0.3-0.8 (1) mm long, usually equal, triangular, rounded or usually acute to acuminate. Corolla tubular to slightly infundibuliform, red to purple, mauve, violet, or lavender, membranaceous to somewhat carnose, glabrous externally, glabrous internally except for a sparse to dense ring

ca. 1-1.5 mm wide of pilose vesture at ca. 1.5-4 mm above the base, or rarely completely glabrous internally; tube 18-32 mm long; lobes 4-12 mm long. Anthers 1.5-2.8 mm long. Styles 18-38 mm long, the stigmatic portion 0.5 mm long. Disk 0.5-0.8 mm high, annular. *Infructescences* similar in size, color, and proportion to inflorescences. *Fruit* 4.5-6 mm long, 5.5-7 mm wide, broadly ellipdsoid to usually ovoid, somewhat didymous, somewhat compressed laterally; pyrene ridges broadly angled.

Additional specimens examined: **JAMAICA.** Without location, without date, *Alexander 21* (GH), 1850 (K, P), *A.G. McCatty s. n.* [Dec 1874] (K), *W. Purdie s. n.* (GH), *Walpor s. n.* (BM), *J. Wolle 9* (GH). CORNWALL. *Hanover*: Dolphin Head, *Adams 8000* (BM, DUKE), *Harris 9240* (A, BM, F, NY, S, US); Dolphin Head, 8 mi SSE by road from Pucea, *Weaver & Weaver 1288* (DUKE). *Trelawny*: Cockpit Country, near Troy, *Britton 645* (NY); Cockpit Country, SW of Windsor Caves, *Crosby & Anderson 1183* (DUKE); Oxford near Troy, *Harris 8659* (BM, F, G, GH, NY, US); Crown lands near Troy, *Harris 8728* (BM, F, NY, S, US); near Troy, *Harris 9246* (NY); Ramgoat Cave district, Cockpit Country, *Howard & Proctor 14389* (A, BM); Crown lands 4 mi W of Troy, *Maxon 2905* (US); Ramgoat Cave district, Cockpit Country, *Proctor 10612* (A, US); Isle View Hill, Wilson Valley district, 1.5 miles N of WARSOP, *Proctor 21352* (GH, NY, US); Mango Tree Hill, *Read 1905* (NY, US); Cockpit Country, beyond Belmore Castle, 1-2 miles NW of Quickstep School, *Webster 5269* (A); Cockpit Country, Crown lands, 4 miles NW of Troy, *Webster et al. 5368* (A, US); Cockpit Country, 3 miles N of Troy, *Webster et al. 8398* (BM, DUKE, F, G, GH, S, US); Cockpit Country, near Ramgoat Cave, NW of Albert Town, *Webster et al. 8443* (G, S); Quickstep, between Belmore Castle and upward, *West & Arnold 276* (GH); top of cockpit hills behind Belle View Castle, Taylor's property, Quick Step Village, District of Look Behind, *Whitefoord 1387* (BM, F); Bunkers Hill, Good Hope, *Whitefoord 1397* (BM). *St. Elizabeth*: Ipswich, *Harris 12368* (BM, F, NY, P, S, US). MIDDLESEX. *St. Ann*: Moneague, Union Hill, *Alexander s. n.* [9 Apr 1850] (K), *Alexander s. n.* [Jun 1850] (NY); Hollymount, *Britton 740* (NY); Union Hill near Moneague, *Britton & Hollick 2768* (NY); road below Hollymount on Mt. Diablo, *Crosby et al. 561* (DUKE); hills or road through Cedar Valley, 1.1 mi E of Clarksonville, G. Goodfriend s. n. [13 Jun 1977] (F); 2.2 mi W of Albion, *Hespenheide et al. 947* (DUKE); below Union Hill, 2.5 miles SSW of Moneague, *Howard & Proctor 13604* (A); Mt. Diablo, *Hunnewell 15362* (GH); vicinity of Hollymount, Mt. Diablo, *Maxon 2211* (NY, US); Mt. Diablo, *H.N. Ridley s. n.* [Feb 1916] (K); lower part of road to Holly Mount; *Stearn 577* (BM); Mt. Diablo, Hollymount Road, *Vuilleumier 89* (A); road from Jamaica A1 to Hollymount on Mt. Diablo, *Weaver & Weaver 899* (DUKE); near Hollymount House, *Weaver & Weaver 979* (DUKE); Mt. Diablo, *Woods 11032* (GH); Fairfield, *Wullschlaegel 840* (M). *Manchester*: Marshall's Pen, 2-2.5 miles due NW of Mandeville, *Bretting J-156* (MO); Marshall's Pen, *Britton 3720* (NY); New Green, *Britton 9699* (NY); vicinity of Mandeville, *Crawford 702* (NY); Marshall's Pen, *Harris 6260* (BM, GH), *Proctor 19680* (NY, US); Denham Farm, near Christiana and Devon, *West & Arnold 908* (GH). *Clarendon*: between Lluidas Vale and Croft Hill, Fosberg 42727 (US); Peckham Woods, *Harris 10956* (F, K, NY, US); Peckingham Woods, *Proctor 10217* (A, NY, US),

Webster & Proctor 5391 (A, BM, DUKE, G, S, US). *St. Catherine*: along limestone ridge 3.5 miles N of Worthy Park, *Webster 13649* (DUKE, GH); Mt. Diablo, Greer Mount, *Webster & Proctor 5633* (BM). SURREY. *St. Thomas*: vicinity of Cinchona, Old England, *Marble 247* (MO, US).

Phenology. Collected in flower in January, March through July and December, and in fruit in March and July through September.

Distribution (Fig. 8). Jamaica, in moist forests, thickets, and cloud forest, 290-800 m.

Palicourea pulchra can be separated from other Antillean species of *Palicourea* by its relatively long tubular corollas with both stamens and style exserted and somewhat didymous usually ovoid fruits. Vegetatively this species resembles *P. croceoides*, which is not known from Jamaica. In both vegetative and floral characteristics *P. pulchra* is similar to *P. wilesii*, with which it was combined for many years and which is also endemic to Jamaica. The distinctions between these are discussed in the treatment of P. wilesii.

Two Marsh specimens of *Palicourea pulchra* at K, both without numbers and both attributed to the Hooker herbarium, are apparently isotypes. One specimen of *P. pulchra* at NY and two at P are attributed only to the Hooker herbarium with no collector's name, and may also be isotypes. The collection data for one specimen, *Harris 9246* (NY), describe the flowers as yellow but this seems questionable.

Var. *hispidula* Proctor is not recognized here. This variety was described based solely on its hispidulous pubescence; the difference between this and the typical variety seems small, especially considering that the range of variation in pubescence among adjacent individuals of other species of *Palicourea* such as *P. alpina*, *P. eriantha*, and *P. croceoides* is larger than that found between these two varieties. *Palicourea pulchra* appears simply to have a range of variation in pubescence among individuals in a population: another collection made at the same locality and time as the type of var. *hispidula*, *Read 1905* (NY!, US!) is only minutely puberulous, and a paratype collection, *Howard & Proctor 14389*, shows both conditions: the specimen at A is hispidulous, while the specimens at BM is only minutely puberulent, similarly to the type specimen.

The flowers of this species are monomorphic with both style and stamens exserted, as discussed in some detail in the introductory section Reproductive Biology.

The relationships of *Palicourea pulchra* within *Palicourea* are not clear. Adams (1972) suggested that *P. pulchra* is related to and perhaps derived form *P. croceoides* or *P. crocea*, which differ primarily in corolla size, corolla and inflorescence color, distyly. *Palicourea pulchra* mores strongly resembles the distylous species *P. lineariflora* Wernham of the northern Andes, both vegetatively and in floral and fruit characters. The relationships of *P. wilesii* are also unclear but this species may be closely related to P. *pulchra*.

7. **PALICOUREA TRIPHYLLA** de Candolle

Prodr. 4: 256. 1830. *Psychotria triphylla* (de Candolle) Mueller Argoviensis in Martius, Fl. bras. 6(5): 233. 1881. TYPE: French Guiana. Without locality, without date, *Patriss. n.* (Holotype: G-DC, microfiche!, photograph NY!). Taylor, 1989: Fig. 20a-c.

Palicourea ternata Urban, Symb. antill. 7: 547. 1913. SYNTYPES: Trinidad. Without location, *Bot. Gard. Herb. 2492* (B), *Fendler 444* (BM!, K!), Aripo Savannah, *D.W. Alexander 5638* (B).

Palicourea elongata Britton, Bull. Torrey Bot. Club 43: 468. 1916. TYPE: Cuba. La Habana: Isla de la Juventud [Isle] of Pines], Las Tunas, *Britton & Wilson 14749* (Holotype: NY!; Isotypes: F!, GH!, MO!, US!).

Erect shrubs or suffrutescent herbs to 2 m tall, glabrate to minutely pilosulous. *Leaves* usually paired or sometimes ternate, the blades 10-23 cm long, 3-9.5 cm wide, ca. 2.3-3 (4.8) times as long as wide, narrowly to broadly elliptic or slightly obovate or lanceolate, acute to acuminate at apex with the tip 5-20 mm long, cuneate to obtuse at base, chartaceous, glabrate or minutely pilosulous above and below, the costa and secondary veins usually prominulous below; secondary veins 8-14 on each side of costa, arched, ultimately paralleling margins, 1 (2) intersecondary veins occasionally present between each pair of secondary veins; margins slightly revolute; petioles 3-10 mm long, vesture similar to that of costa. Stipules forming a continuous sheath, glabrate to pilosulous; sheath 1-2 mm long, the lobes 4-11 mm long, lanceolate, acute, ciliate. *Inflorescences* 7-16.5 cm long, 2-4 cm broad, ca. 2-4.5 times as long as broad at the base, narrowly pyramidal to nearly cylindrical; bracts 0.5-15 mm long, narrowly triangular to linear, ciliate, those subtending primary branches ca. 4-15 mm long, those subtending pedicels ca. 0.5-1 mm long; bracteoles and colleters absent; peduncles 6-10.5 cm long, not geniculate at base; pedicels 1-5 mm long; peduncle, axis, branches, bracts, and pedicels yellow, minutely pilosulous or hispidulous. *Flowers* monomorphic, similar to long-styled form. Calyx yellow, minutely pilosulous; limb divided for ca. 1/2 its length, the lobes 0.5-0.8 mm long, usually equal, broadly triangular, obtuse, ciliolate. Corolla tubular to slightly infundibuliform, gibbous at base, yellow, membranaceous, puberulent externally with stout red or brown hairs, glabrous internally except for a ring ca. 1 mm wide of pilose vesture at ca. 1/5 the length of tube above base; tube 9-10 mm long; lobes 1.5-2 mm long. Anthers 3 mm long. Style ca. 8 mm long, the stigmatic portion 2.5 mm long. Disk 0.7 mm high, annular. *Infructescences* similar in size and proportion to inflorescences, becoming purple. *Fruit* 4 mm long and wide, ovoid, compressed laterally, glabrate to sparsely pilosulous; pyrene ridges sharp.

Additional specimens examined: CUBA. Without location, *Wright 2756* (BM, G(2), GH, K, MO, P, S). PINAR DEL RIO: Los Almácigos y Consolación, *Wright 229* (NY); Herradura, *Eagle 727* (A, F); Sierra de Los Organos, grupo del Rosario, Loma Pelada, *Ekman 17616* (F, G, NY, S); on road from Viñales to La Baliza near La Constancia copper mine, *Ekman 17958* (A, BM, S, US); Pinar del Río City, at Km 13 of the high road to Coloma, *Ekman 18236* (S). LA HABANA: Isla de la Juventud [Isle of Pines], *A.A. Taylor 202* (F, NY); Oakland arroyo, *Britton & Britton 7534* (NY); San Pedro and vicinity, to Arroyo, *Britton et al. 15785* (NY, US); near San Francisco in thickets at Río Mal País, *Ekman 11890* (S); Los Indios, *Jennings 332* (NY); Cañada La Ceiba, *León & Marie-Victorin 18872* (NY). VILLE CLARA [formerly Las Villas]: Trinidad Mountains, *Howard 5298* (NY). SANCTI-SPIRITUS [formerly Las Villas]: Buenos Aires, Trinidad Mountains, *Howard 5226* (GH).

Phenology. Collected in flower in February, March, May, and July, and in fruit in March, May, June, October, and November.

Distribution (Fig. 6). Caribbean lowlands of southern Mexico and Central America to southern Brazil, and in central and western Cuba, in moist to wet ground, 0-1300 m.

This species can be separated from other Antillean Palicoureas by its lanceolate stipule lobes. Most but not all of the Cuban plants have binate leaves, in contrast to mainland populations in which the plants more frequently have ternate leaves. *Palicourea* elongata was originally separated based on its paired leaves.

Mainland populations of *P. triphylla* are distylous, but only one style form has been seen in the Cuban specimens. This resembles the long-styled form of distylous species. Relatively few collections have been seen, none more recent than the first half of this century, so it is possible that the Cuban populations are actually distylous and are more widespread than indicated here.

The Cuban plants are probably most closely related to conspecific Mexican and Central America populations. *Palicourea triphylla* appears to be most closely related to several other South American *Palicourea* species with similar aspect and fruit, notably *P. calophylla* de Candolle and *P. tetraphylla* Chamisso & Schlechtendel.

8. PALICOUREA WILESII C.D. Adams

Phytologia 21(2): 68. 1971. TYPE: Jamaica. Without location, without date, *J. Wiles s. n.* (Holotype: BM!). Fig. 9.

Erect shrubs to 4 m tall, glabrous or minutely puberulous. *Leaves* paired, the blades 7-16 cm long, 1.8-6 cm wide, ca. 2.5-3.7 times as long as wide, elliptic, acute to acuminate at apex with the tip 5-15 mm long, acute at base, chartaceous, glabrous or minutely puberulous; secondary veins 7-12 on each side of costa, broadly curved, 1 (3) intersecondary veins usually present between each pair of secondary veins; margins straight; petioles 5-18 mm long, with vesture similar to that of costa. Stipules forming a continuous sheath, glabrous; sheath 0.5-1 mm long, the lobes 2.5-4 mm long, triangular, acute. *Inflorescences* 3.2-6.5 cm long, 3-8 cm broad, ca. 0.6-1.5 times as long as broad (0.7-1.7 times as broad as long) at base, pyramidal; bracts 0.5-7 mm long, triangular, acute, those subtending primary branches ca. 2-7 mm long, those subtending pedicels ca. 0.5-1 mm long, bracteoles and colleters absent; peduncles 1.5-6.5 cm long, not geniculate at base; pedicels 1-5 mm long; peduncle, axis, branches, bracts, and pedicels red-purple, glabrous to minutely puberulous. *Flowers* monomorphic, similar to long-styled form. Calyx red-purple, glabrous to minutely puberulous; limb divided to the base, the lobes 0.3-1 mm long, usually equal, triangular, rounded to acute or acuminate. Corolla tubular to somewhat infundibular, red-purple or white flushed with red-purple, somewhat carnose, glabrous externally and internally except for a ring ca. 0.5-1 mm wide of pilose vesture at ca. 1.5 mm above the base of the tube; tube 11-16 mm long; lobes 1.8-3 mm long. Anthers 1.8-2.2 mm long. Style 12-20 mm long, the stigmatic portion ca. 0.5 mm long. Disk 0.5-0.8 mm high, annular. *Infructescences* similar in size, color, and proportion to inflorescences. *Fruit* 4-4.5 mm long, 4-5.5 mm wide, elliptic, somewhat didymous, somewhat compressed laterally; pyrene ridges

sharply angled.

Additional specimens examined: **JAMAICA.** Without location, without date, *Forster s. n.* (K), *Walpers s. n.* (BM); Whitfield Hall, *Harris 6312* (F, MO, US). CORNWALL. *St. James*: Pembroke, Silver Gove, Flagstaff, Maroon Town, 18°21'30"N, 77°46'30"W, *Osmaston 5008* (BM). *Trelawny*: Crown lands 4 miles W of Troy, *Maxon 2881* (NY, US), 2905 (US). MIDDLESEX. *Clarendon*: along road between Ritchies and Balcarres, *Proctor 33782* (NY). SURREY. Blue Mountains, *Harris 5180* (G, US), *5203* (BM, G, GH, US). *St. Andrew*: Greenwich Bridle Road, *Adams 7475* (BM, DUKE), *7486* (M); Flamstead and vicinity, Port Royal Mountains, *Maxon 8678* (GH, NY, US); upper S slope of Silver Hill Gap, *Proctor 23278* (GH). *Portland*: Lawrence Bottom, *Adams 7910* (DUKE, M); Silver Hill, *Adams 11926* (BM); trail N and W of Silver Hill Gap, *Hespenheide et al. 805* (DUKE). *St. Thomas*: SE slopes of Stone Hole Bump, *Maxon 9036* (GH, NY, US); John Crow Mountains, E slope, 1.5 mi SW of Ecclesdown, *Webster* & *Wilson 5139* (A).

Phenology. Collected in flower from May through August, and in fruit in December.

Distribution (Fig. 8). Jamaica, in moist and wet forests, 323-1140 m.

Palicourea wilesii resembles P. *pulchra*, which also grows in Jamaica and was combined with it for many years. *Palicourea wilesii* can be separated by its corollas, with tubes 11 to 16 mm long and spreading lobes 1.8 to 3 mm long in contrast to tubes 18 to 32 mm long and strongly recurved lobes 4 to 12 mm long in *P. pulchra*. The anthers are only partially exserted in *P. wilesii* in contrast to fully exserted in *P. pulchra*. Vegetatively and in fruit these species are difficult to distinguish. *Palicourea wilesii* is also similar to *P. croceoides*, which is not known from Jamaica.

Adams (1972) gives a higher elevational range for this species than presented here, to 3750 feet (1210 m), but no specimens have been seen. He also states that *Palicourea wilesii* "replaces P. *pulchra* in eastern Jamaica", but the ranges of these species as circumscribed here overlap. The circumscription of these species here is based on the relative lengths of the corolla tubes and lobes and the position of the anthers, and may be somewhat different from that of Adams, who used overall corolla length.

The relationships of P. wilesii to other species of *Palicourea* are not clear. It may be closely related to *P. croceoides* or *P. crocea*, as suggested by Adams (1972); these species differ primarily in corolla and inflorescence color. It may also be related to P. *pulchra*.

Excluded Species

PALICOUREA BRACHYSTIGMA Urban

Ark. Bot. 17(7): 58. 1921. TYPE: Hispaniola. Haiti. Sud: in montibus Ma Blanche, 1400 m, Aug, *Ekman 505* (Holotype: B, destroyed; Isotype: S!).

= *Psychotria* subg. *Heteropsychotria* Steyermark.

PALICOUREA CYANEA Urban

Symb. antill. 9: 168. 1923. TYPE: Cuba. Pinar del Río: in Sierra de los Organos prope San Diego de Tapias, Apr, *Ekman 10637* (Holotype: B, destroyed; Isotype: NY!).

= *Psychotria toensis* Britton & Wilson.

PALICOUREA DIDYMOCARPA (A. Richard) Grisebach
Cat. pl. Cub. 138. 1866. *Ronabea didymocarpa* A. Richard, Mem. Soc. Hist. Nat. Paris 5: 170. 1830. TYPE: not designated.
= *Psychotria bahiensis* de Candolle (Steyermark, 1974).

PALICOUREA DOMINGENSIS (Jacquin) de Candolle
Prodr. 4: 529. 1830.
= *Psychotria domingensis* Jacquin. (Taylor, 1987).

PALICOUREA MICRANTHA Urban & Ekman
Ark. Bot. 22A (10): 96. 1929. TYPE: Hispaniola. Dominican Republic. Azua: Cordillera Central prope Las Lagunas, 750 m, Jun, *Ekman H6410* (Holotype: B, destroyed; Isotyped: S!).
= *Psychotria* subg. *Heteropsychotria* Steyermark.

PALICOUREA PATENS (Swartz) Urban
Feddes Repert. Spec. Nov. Regni Veg. 18: 197. 1922.
= *Psychotria deflexa* de Candolle (Steyermark, 1974).

PALICOUREA PAVETTA (Swartz) de Candolle
Prodr. 4: 525. 1830.
= *Psychotria domingensis* Jacquin (Taylor, 1987).

PALICOUREA PURPURASCENS Urban
Symb. antill. 9: 167. 1923. TYPE: Cuba. Granma [formerly Oriente]: in Minas de Iberia in cacumine Sierra Maestra ad Tacobay, 800 m, Dec, *Ekman 3779* (Holotype: B, destroyed; Isotypes: F!, G!, NY!, S!).
= *Psychotria toensis* Britton & Wilson.

PALICOUREA TABERNAEFOLIA (Poiret) de Candolle
Prodr. 4: 525. 1830.
= *Psychotria domingensis* Jacquin (Taylor, 1987).

PALICOUREA TOENSIS (Britton & Wilson) Standley
Field Mus. Nat. Hist., Bot. Ser. 11: 231. 1936. TYPE: Cuba. Granma [formerly Oriente]: Río Yamaniguey to Camp Toa, *Shafer 4009* (Holotype: NY!; Isotypes: A!, NY!).
= *Psychotria toensis* Britton & Wilson, Mem. Torrey Bot. Club 16: 113. 1920.
This species lacks the swollen base closed by a pilose internal ring that characterizes the corollas of *Palicourea*. Although the corolla is pubescent internally, the trichomes are situated not at the base of the straight tube but at the straight attachment, which describes *Psychotria* rather than *Palicourea* (Taylor, 1989).

PALICOUREA TORBECIANA Urban & Ekman

Ark. Bot. 21A(5): 87. 1927. TYPE: Hispaniola. Haiti. Sud: Massif de LaHotte in parte occidentali prope Torbec in montibus supra La Mare Proux, 1200 m, Dec, *Ekman H5270* (Holotype: B, destroyed; Isotype: S!).

= *Psychotria* subg. *Heteropsychotria*.

PALICOUREA UMBELLATA de Candolle

Prodr. 4: 526. 1830.

This name was originally applied to a species from French Guiana that is now called *Palicourea quadrifolia* (Rudge) de Candolle (Steyermark, 1972). Grisebach reported *P. umbellata* from Trinidad; Urban (1912) cited Grisebach's usage of this name in synonymy with *Psychotria acuminata* Bentham (now called *Psychotria bahiensis* de Candolle; Steyermark, 1972), with the comment that it differed from that of de Candolle. The name *Palicourea umbellata* was doubtfully and incorrectly applied by Stahl (1937) to a plant found in Puerto Rico. This plant is difficult to identify from his description, but is certainly not a *Palicourea* (it seems most likely to be *Psychotria pubescens* Swartz).

Acknowledgements

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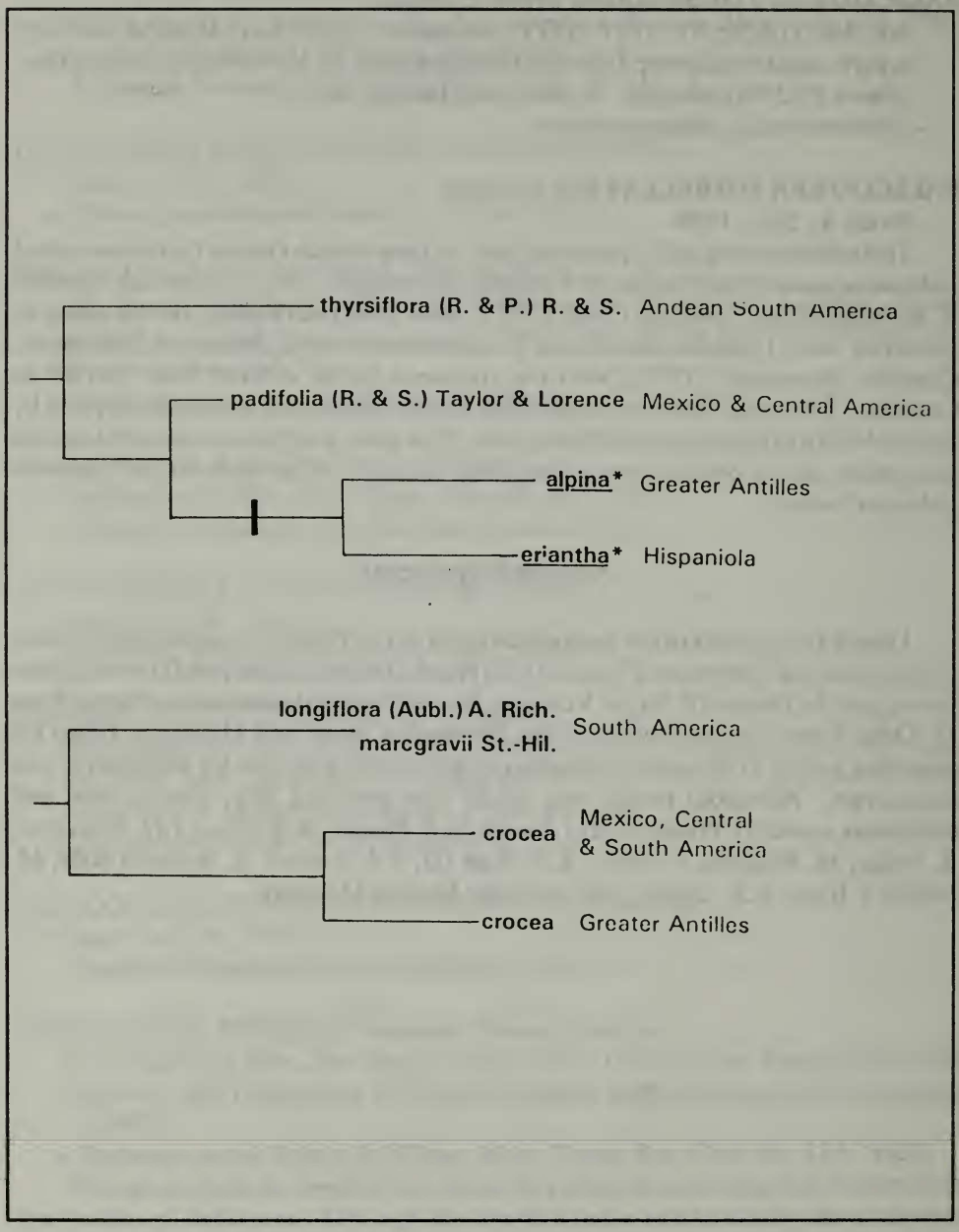


Fig. 1 Putative relationships of West Indian *Palicourea* to mainland South and Central American *Palicourea*. Asterisks indicate monomorphic flowers; black bars indicate hypothesized loss of distyly; endemic West Indian species are underlined. The hypothesized relationships of these species are discussed after each description; the probable colonization routes are discussed in the introductory section.

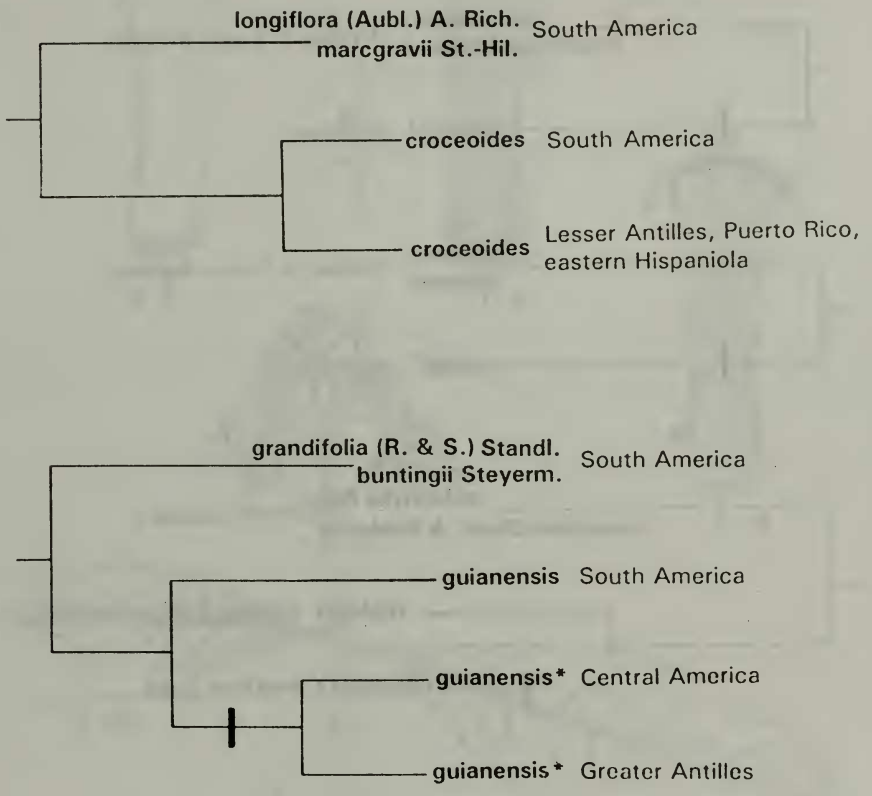
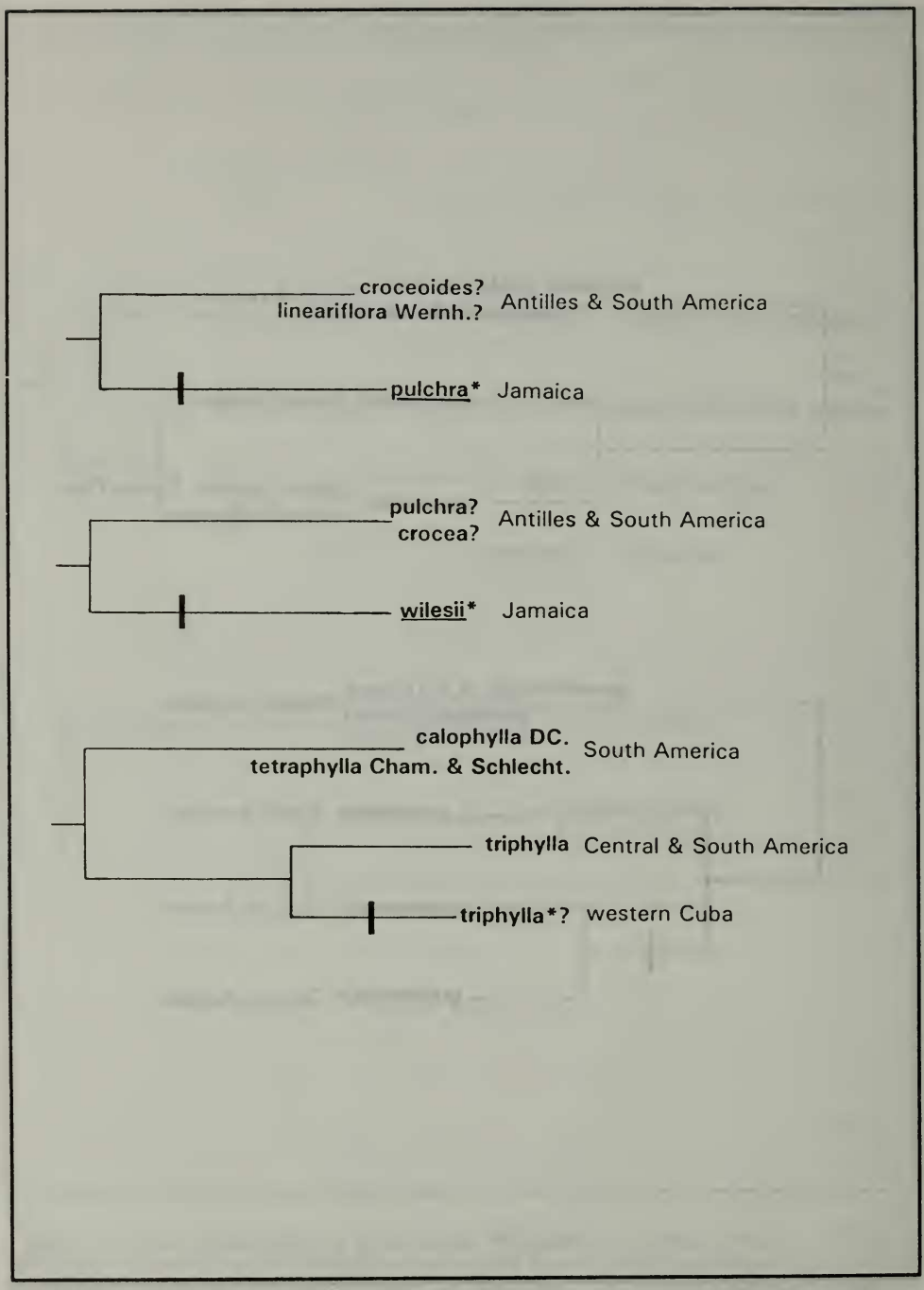


Fig. 1 (Continued)



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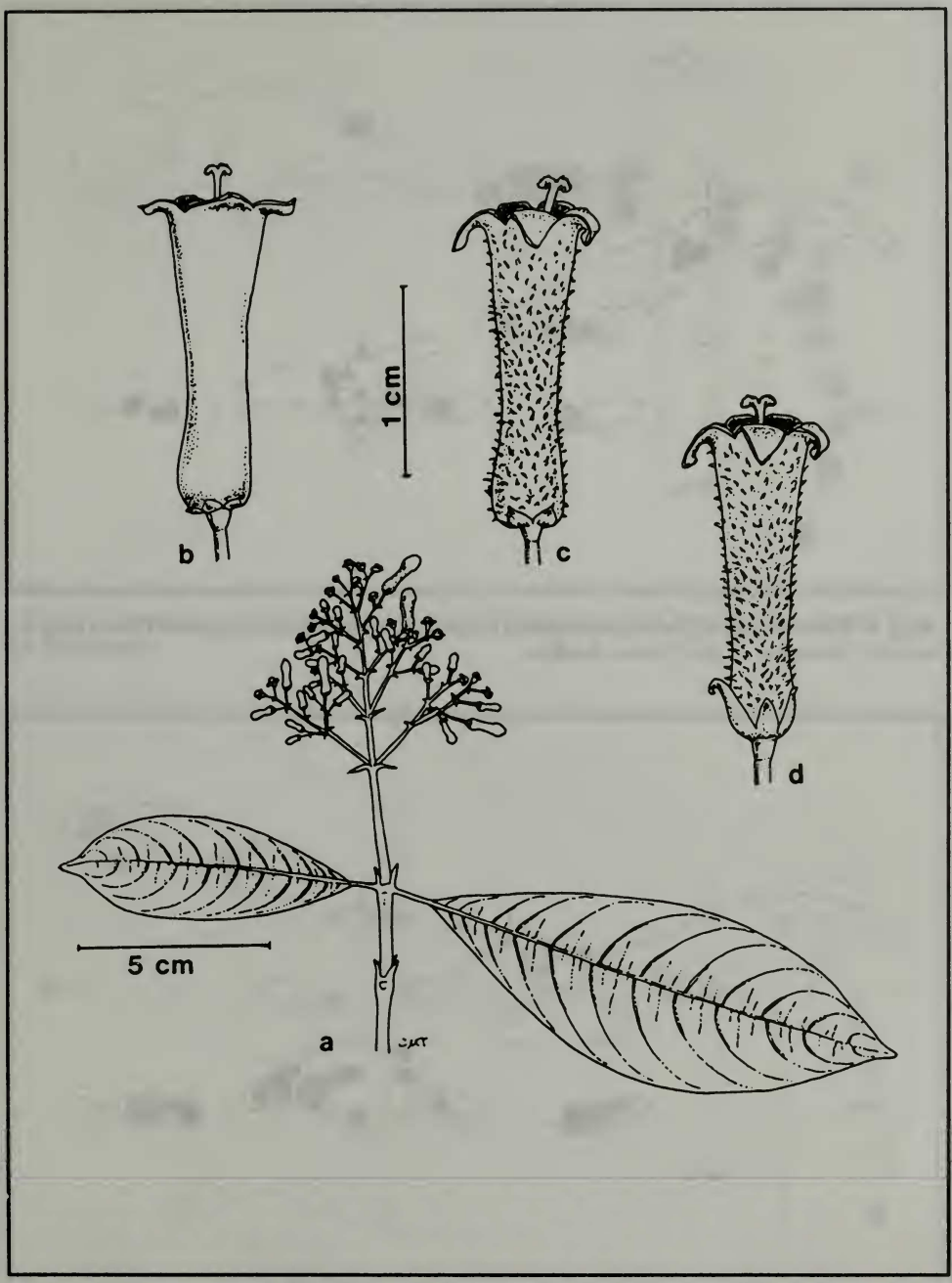

Fig. 2 ***Palicourea alpina*** (Swartz) de Candolle and ***P. eriantha*** de Candolle. Palicourea alpina: a, flowering branch. b, glabrous mature flower. c, pubescent mature flower. ***Palicourea eriantha***: d, mature flower. b, c, d to same scale.

Fig. 3 Distribution of *Palicourea alpina* (Swartz) de Candolle (circles) and *P. eriantha* de Candolle (triangles) in the Greater Antillas.

Fig. 4 Distribution of *Palicourea* crocea (Swartz) Roemer & Schultes in the Greater Antilles.

Fig. 5 Distribution of *Palicourea croceoides* W. Hamilton in the Lesser Antilles, Puerto Rico, and Hispaniola.

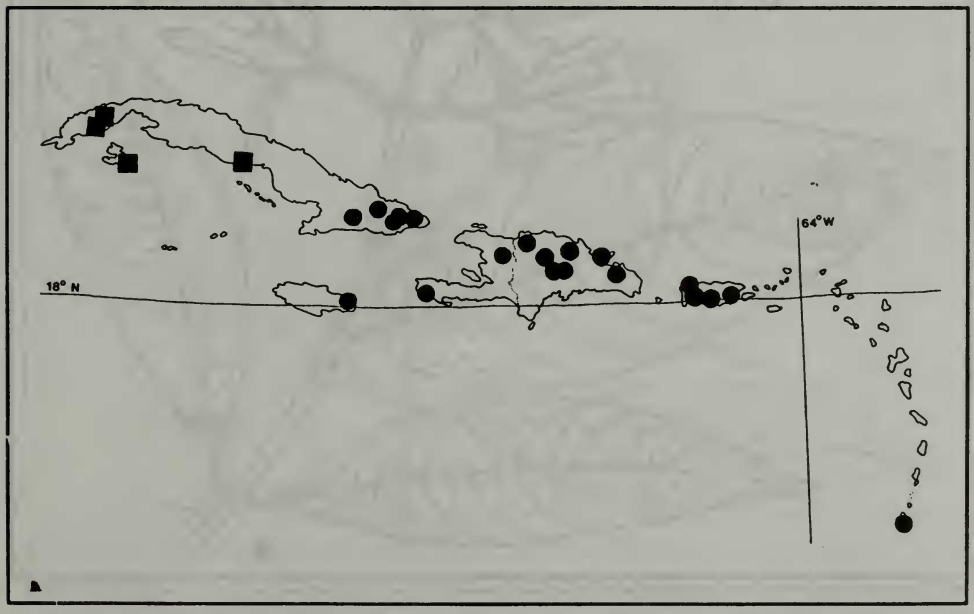

Fig. 6 Distribution of *Palicourea guianensis* Aublet (circles) and *P. triphylla* de Candolle (triangles) in the Antilles.

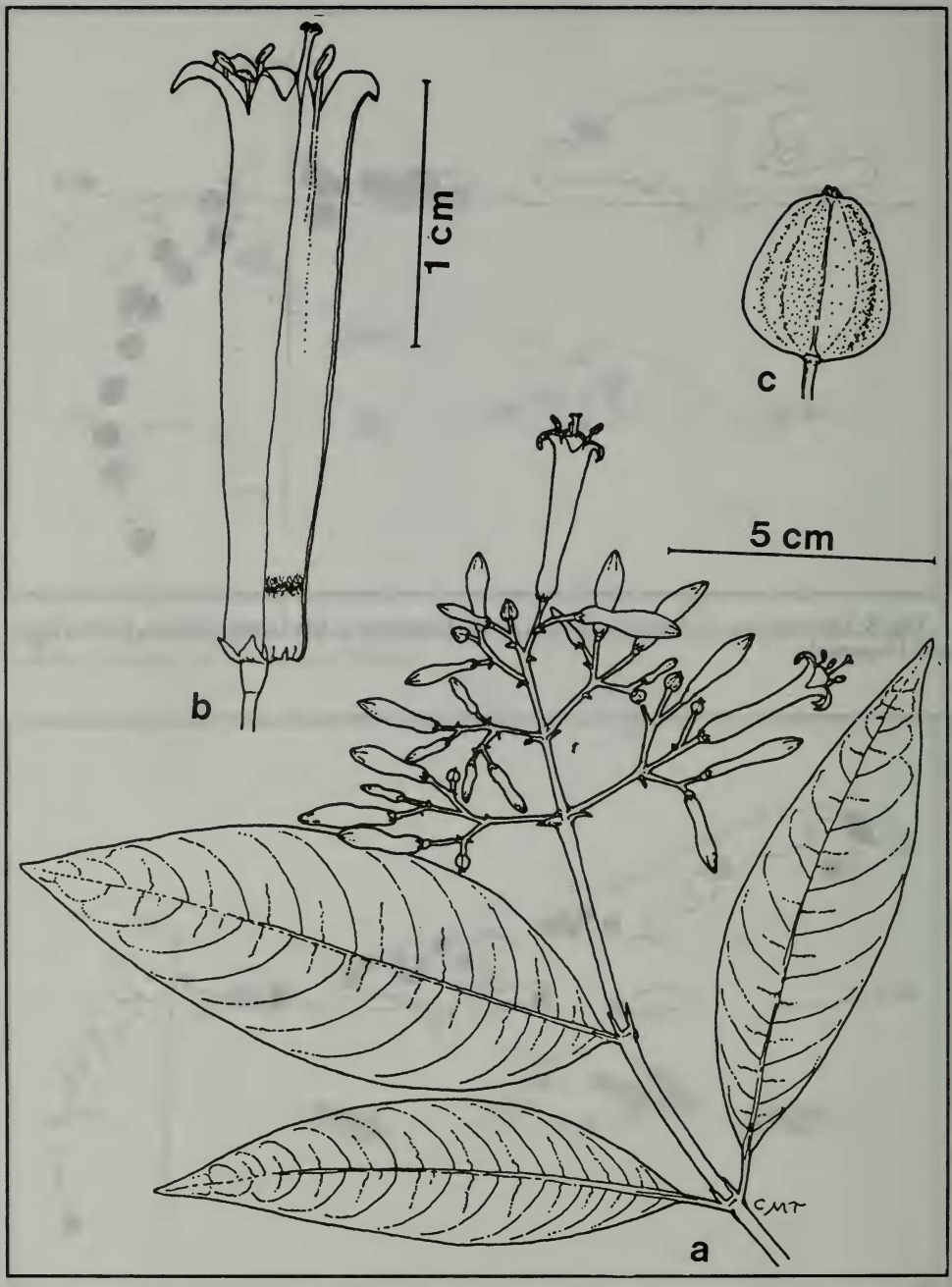

Fig. 7. *Palicourea pulchra* Grisebach. a, flowering branch. b, mature flower, partially opened. c, dry immature fruit. b, c to same scale.

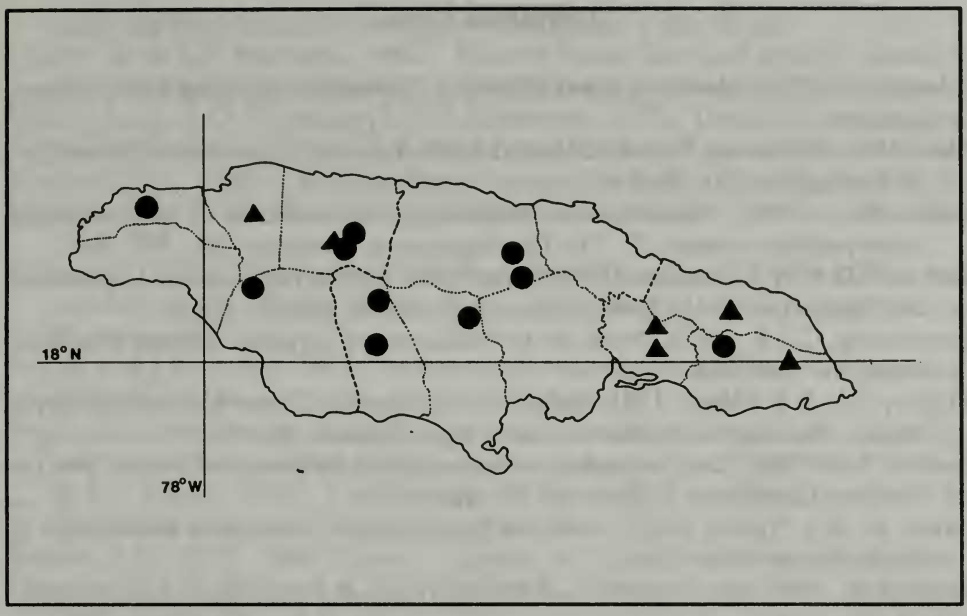

Fig. 8 Distribution of *Palicourea pulchra* Grisebach (circles) and P. *wilesii* C.D. Adams in Jamaica.

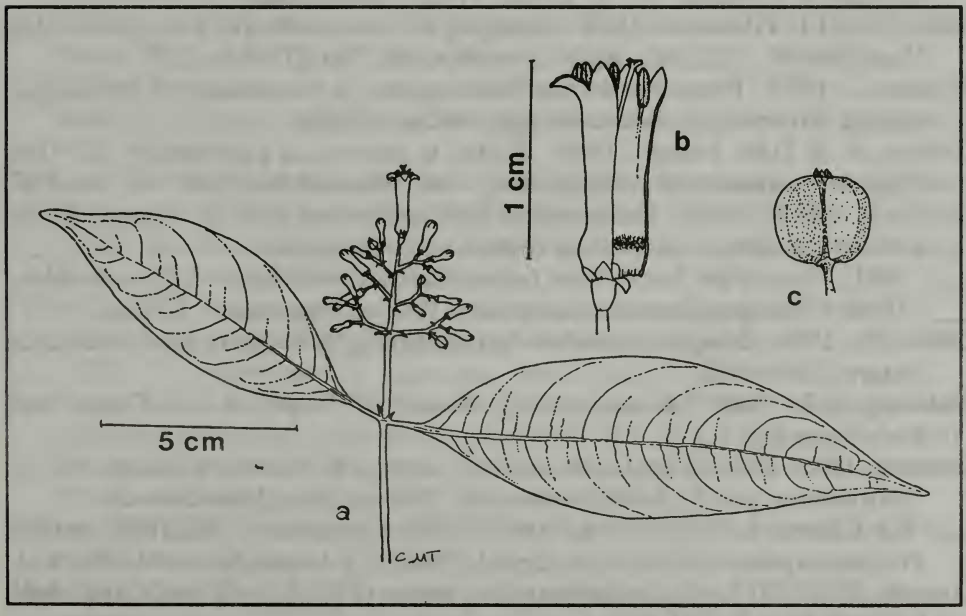

Fig. 9 *Palicourea* wilesii C.D. Adams. a, flowering branch. b, mature flower, partially opened. c, dry immature fruit. b, c to same scale.

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Index to Numbered Collections of *Palicourea* from the West Indies

Collections are cited under the name of the principal collector only. Many other collections seen, including historically important specimens, are not included here because they were not numbered. An asterisk denotes type collections. Each collection is identified by species number after it in parenthesis, as follows:

1. *P. alpina*
2. *P. crocea*
3. *P. croceoides*
4. *P. eriantha*
5. *P. guianensis*
6. P. *pulchra*
7. *P. triphylla*
8. P. wilesii

Abbot, W.L. 88 (2), 252 (3), 2156 (5).
Acevedo, P. 69 (2).
Acuña, J.B. 6770 (1), 9895 (1), 13367 (5).
Adams, C.D. 5868 (1), 6443 (1), 7475 (8), 7476 (1), 7486 (8), 7910 (8), 8000 (6), 9071 (5), 9219 (2), 9284 (2), 11926 (8).
Agosto, B. 151 (2), 241 (2), 485 (2), 896 (2).
Alexander, D.W. 5638* (7).
Alexander, R.C. 21 (6).
Allard, H.A. 13819 (2), 13994 (2), 18261 (5), 18297 (5), 18298 (5).
Anderson, W.R. 3205 (1).
Bailey, L.H. 303 (3).
Barry 1082 (1).
Beard, J.S. 182 (3).
Beard, P. 1051 (3), 1242 (3), 1373 (3).
Belanger, C.P. 143 (3), 145 (3).
Béna, P. 1029 (3), 1030 (3), 1031 (3), 1032 (3), 1033 (3), 1034 (3), 1036 (3), 1077 (3), 1082 (3), 1103 (3), 1104 (3), 1323 (3), 1531 (3), 1556 (3), 1570 (3), 2244 (3), 2384 (3).
Blauner, B.F. 97 (3).
Bordas 62 (3).
Box, H.E. 1059 (3), 1838 (3).
Bretting, P.K. J-156 (6).
Britton, E.G. 1891 (2).
Britton, N.L. 67 (1), 112 (3), 172 (1), 175 (3), 379 (2), 536 (3), 645 (6), 693 (2), 740 (6), 782 (3), 820 (3), 1397 (3), 1449 (2), 1573 (2), 1611 (3), 1622 (2), 1804 (1), 2178 (3), 2386 (2), 2594 (3), 2768 (6), 3323 (1), 3553 (2), 3720 (6), 3925 (3), 4202 (2), 4264 (2), 5317 (1), 5427* (1), 6272 (2), 6309 (2), 6703 (3), 6787 (2), 6888 (2), 7290 (1), 7534 (7), 7661 (3), 8168 (3), 8369 (3), 9699 (6), 9906 (3), 9907 (2), 9978 (3), 14463 (2), 14749* (7), 15785 (7).
Buch, W. 834 (4).
Burch, D. 1373 (3), 3201 (3).

Cabanillas 1552 (2).
Carabia, J.P. 3672 (5).
Cobin 1138 (3), 1188 (1).
Cook, O.O. 162 (2), 446 (2).
Cooley 8219 (3), 8785 (3), 8962 (3).
Cooper, G.P. 6 (3).
Cowan, R.S. 1573 (3).
Crawford 702 (6).
Crosby, M.R. 319 (2), 376 (1), 561 (6), 896 (1), 1073 (2), 1183 (6).
D'Arcy, W.G. 139B (3), 369 (3), 370 (3).
Deffenrand, C. 4523 (3).
DeWolf 1898 (3).
Díaz, L. 20 (1).
Duke, J. 7312 (3), 7370 (1), 7400 (3).
Duss, A. 316 (3), 602 (3), 2530 (3).
Earle, F.S. 727 (7).
Eggers, H.F.A. 400 (2), 460 (2), 959 (3), 1049 (5), 1236 (3), 1694 (2), 2209 (4), 5032 (5), 5034 (1), 6074 (3), 6390 (3), 6887 (3).
Ekman, E.L. 1651 (1), 3773a (5), 3773b (5), 4123 (2), 5196 (2), 5282a (1), 5493 (1), 5800 (2), 6194 (2), 6853 (5), 6953 (1), 8751 (1), 10310 (1), 11890 (7), 13913 (1), 14211 (1), 15938 (5), 16071 (1), 16717 (2), 17616 (7), 17958 (7), 18236 (7). H591 (1), H1280 (4), H1561 (4), H2618 (2), H5139 (4), H5306 (4), H6233 (5), H8626a (2), H8626b (1), H9944 (5), H10236 (5), H11067 (2), H11556 (5), H12863 (4), H15092 (3).
Evans, L. 142 (3).
Eyerdam, W.J. 177 (1), 457 (2).
Faris, J.A. 8401 (2).
Fawcett, W. 8025a (2).
Feinsinger, P. 108 (3).
Finch, R.G. 11 (3), 31 (3).
Fishlock, W.C. 94 (3), 363 (3).
Fortuna 77 (2).
Fosberg, F.R. 42839 (1), 42727 (6), 48301 (3).
Fredholm, A. 3147 (2).
Fuertes, M. 335 (2), 1648 (4), 1948b (4).
Funck, N. 65 (3).
García 682 (2), 1154 (4), 1172 (4).
Gastony, G.J. 171 (4), 402 (4), 539 (4).
Gentry, A. 50377 (3), 50382 (3), 50383 (2).
Gillis, W. 8160 (3).
Goll, G.P. 416 (3), 446 (2).
González 565 (1), 2742 (3).
Gregory, L.E. 802 (2).

Grosourdy, R. de 43 (2).
Hahn, L. 427 (3), 525 (3), 802* (3).
Hansen, C.O.E. 9054 (3).
Harris, J.A. C15174 (1), C15206 (1), C15261 (1), C15481a (1).
Harris, W. 5180 (8), 5203 (8), 6260 (6), 6312 (8), 8659 (6), 8728 (6), 9116 (1), 9240 (6), 9246 (6), 9435 (2), 10563 (1), 10956 (6), 12368 (6).
Hart, J. 894 (1).
Hartley, T.G. 13361 (3).
Heller, A.A. 131 (2), 274 (3), 1093 (3), 4377 (2), 4540 (2), 6408 (3).
Hernández, 4-313 (2).
Hespenheide, H.A. 416 (3), 463 (3), 544 (3), 700 (1), 805 (8), 947 (6), 1432 (1).
Hioram 4232 (5).
Hodge, W.H. 685 (3), 686 (3), 687 (3), 699 (3), 1188 (3), 1298 (3), 1498 (3), 2601 (3), 3406 (3), 1660 (3), 1929 (3), 2585 (3), 2818 (3), 3562 (3).
Holdridge, L.R. 135 (3), 807 (4), 648 (2).
Howard, R.A. 5226 (7), 5298 (7), 9364 (4), 11168 (3), 11295 (3), 11661 (3), 11737 (3), 11888 (3), 12573 (4), 13604 (6), 14389 (6), 14991 (2), 15091 (3), 15145 (3), 15208 (3), 15416 (1), 15426 (1), 15772 (3), 16885 (3), 16983 (2), 17495 (3), 17525 (3).
Hunnewell, F.W. 15362 (6), 19283 (3), 19538 (2 & 5).
Jack, J.G. 5982 (1), 7416 (1), 8061 (1).
Jaeger, E.C. 163 (4).
Jennings, O.E. 332 (7), 413 (2).
Jérémie, J. 13 (3), 72 (3), 209 (3), 354 (3), 431 (3), 735 (3), 1446 (3).
Jiménez, J. de J. 1146 (2), 3026 (1), 4501 (4), 4233 (2), 5031 (3), 5804 (5).
Johnston, J.R. 162 (2).
Judd, W.S. 529 (1), 1526 (4).
Kadsworth, R.K. 200 (3).
Killip, E.P. 43779 (2), 45684 (2).
Kuntze, O. 245 (2).
Lamentin 2255 (3).
León, J.S.S. 4042 (1), 4979 (2), 6632 (1), 7878 (1), 8448 (2), 9442 (2), 9857 (1), 9870 (1), 11014 (1), 12172 (1), 18872 (7), 20580 (1).
Leonard, E.C. 4360 (4), 7836 (2), 9654 (2).
Liogier, A. 9068 (2), 9430 (1), 9450 (1), 9633 (3), 9836 (2), 9922 (2), 9997 (1), 10127 (3), 10166 (2), 10530 (3), 10815 (1), 11369 (4), 11539 (4), 11853 (2), 11949 (4), 15838 (2), 18760 (2), 19003 (2), 19777 (4), 21604 (2), 23517 (1), 23542 (4), 25374 (2), 25519 (5), 25749 (4), 26050 (2), 26663 (2), 28098 (3), 28125 (2), 28270 (1), 29801 (2), 32697 (2), 33036 (3), 33099 (1), 34383 (1), 35094 (1), 35099 (1), 35599 (2), 35882 (1), 36551 (1).
Little, E.L., Jr. 13041 (3), 13681 (1), 14804 (3), 14805 (3), 14816 (1), 14845 (1), 14902 (3), 16321 (1), 21605 (3), 21751 (1), 21903 (3), 21907 (3), 25725 (5), 25726 (2 and 3, mixed); 26173 (5), 28153 (3), 28098 (3), 29846 (3), 29879 (3), 30388 (3), 30959 (3), 33036 (3).

Lloyd, F.E. 10 (3), 667 (3), 906 (3).
López Figueiras, M. 209 (5), 477 (1), 1101 (1), 2777 (1).
LeBrón-Luteyn, M. 11470 (2).
Marble 247 (6).
March, W.T. 628 (2), 633 (2), 637 (2), 638 (2), 1351 (2), 1851 (2).
Marie-Victorin, J.C.K. 125 (2), 60059 (2).
Martorell, L.F. 4148 (3).
Maxon, W.R. 623 (1), 1783 (2), 2211 (6), 2681 (1), 2881 (8), 2905 (8), 8678 (8), 9036 (8), 9243 (1), 9463 (1), 9666 (1), 9826 (1), 10019 (1).
Mejía, M. 298 (1), 521 (4), 807 (2), 927 (4), 1397 (2), 2006 (3), 2030 (1), 6396 (2), 6601 (2), 6943 (2), 6985 (4), 7598 (4), 7918 (2), 7987 (2), 8035 (2), 8702 (4), 9633 (2), 9899 (2), 10149 (2), 10198 (2), 10497 (2), 10539 (2), 11106 (2), 11119 (2), 11992 (2), 23371 (2).
Melo, 215 (2).
Miller, G.S. 7 (3), 15 (3), 1094 (2), 1218 (5), 1497 (2).
Millspaugh, C.F. 1970 (2).
Mitchell, A. 10071 (5).
Monachino, J. 747 (1).
Mori, S. 17039 (3).
Morse, 5 (3).
Morton, C.V. 3423 (1), 3449 (5), 3681 (1), 4477 (2), 5113 (3), 5582 (3), 9283 (1), 9354 (1), 9357 (1), 9367 (1).
Mouret, M. 382 (3).
Nash, G.V. 269 (2), 278 (2).
Orcutt, C.R. 2070 (2).
Osmaston, H.A. 5008 (8), 5104 (1).
Otero, J.I. 9 (2), 549 (3), 747 (1).
Pelaez 692 (2), 1882 (4).
Perkins 1382 (2), 1475 (1).
Perottet 240 (3).
Philipson, W.R. 645 (2), 709 (1).
Plée, A. 449 (5).
Prance, G.T. 29315 (3), 29360 (3).
Price, W.R. 331 (3).
Prior, A. 448 (1).
Privault, D. 12 (3).
Proctor, G.R. 9446 (1), 10008 (2), 10217 (6), 10463 (1), 10612 (6), 10806 (4), 10893 (4), 15554 (1), 15847 (2), 16906 (3), 17577 (3), 17882 (3), 18168 (3), 18844 (3), 19460 (3), 19680 (6), 21352 (6), 22091 (5), 23278 (8), 23910 (1), 23955 (2), 28414 (1), 31069 (5), 33782 (8), 41717 (3).
Quentin 412 (3).
Questel, A. 4972 (3).
Ramsammy, J.R. 80 (3).
Read, R.W. 1793 (2), 1904* (6), 1905 (6), 1991 (1).

Riedlé, A. 92 (5), 219 (5).
Rodríguez, L. 3400 (3), 3516 (3), 3710 (3), 3947 (3), 4445 (3).
Rodríguez, M. 46 (1).
Rohr, J.P. von 125 (3).
Rose, J.N. 4325 (2).
Rothrock, J.T. 32 (1).
Sánchez 89 (4).
Sanders 1482 (3).
Sargent, F.H. B166 (3), 120 (2).
Sastre, C. 1846 (3), 1905 (3), 7202 (3).
Sauer 4308 (3).
Schomburgk, R.H. 64 (4).
Schubert, B. 420 (3).
Seifritz, W. 1099 (1).
Shafer, J.A. 185 (3), 686 (3), 1141 (3), 3148 (2), 3282 (1), 3888 (5), 4378 (5), 8599 (1), 9037 (1), 13575 (2).
Shillingford, C.A. 25 (3).
Sieber, F.W. 80 (3).
Sinha 1066 (1).
Sintenis, P. 64 (2), 64b (2), 279 (5), 1267 (3), 1291b (3), 1684 (3), 1685 (3), 2560 (2), 2686 (1), 2757 (3), 2874 (2), 3071 (3), 4613 (1), 5154 (2), 5200 (3), 5944 (5), 6048 (3), 6048b (2), 6202 (5).
Skog, L.E. 1532 (2).
Slane 1 (3).
Smith, A.C. 10188 (4), 10301 (3), 10120 (3), 10339 (3), 10502 (3), 10543 (3).
Smith, H.H. 334 (3).
Sohmer, S. 9602 (4).
Soller 15 (2), 18 (2).
Solomon 5669 (3).
Stahl, A. 724 (5).
Stearn, W.T. 577 (6).
Stehlé, H. 33 (3), 1506 (3), 2136 (3), 2376 (3), 2642 (3), 4652 (3), 5566 (3), 6001 (3), 6218 (3), 6412 (3), 6847 (3), 6930 (3).
Stevens, F.L. 1055 (2), 1728 (3), 2762 (3), 7257 (2).
Stevenson, J.A. 1754 (3), 2369 (3), 2370 (2).
Stimson, W.R. 1220 (2), 1575 (1), 1973 (2), 3517 (3), 3722 (1).
Sturrock 191 (3).
Swartz, O. 431 (1).
Taylor, A.A. 74 (2), 202 (7).
Taylor, C.M. 6128 (3).
Terborgh, J. 243 (2), 256 (5), 334 (3).
Thompson, J. 8025 (2).
Tuerckheim, H. von 2990 (4), 3318 (4), 3743 (A, F, G, GH, MO, P, S, US, 2; G, K, NY, 5).

Underwood, L.M. 102 (2), 1402 (5).
Valeur, E.J. 15 (4), 524 (5), 1014 (2), 1020 (4).
van Hermann, H.A. 711 (2).
Villegas 37 (2).
Vivaldi, J. 72-97 (1), 29801 (1).
Votava, F. 7 (2).
Votava, F. & A. Liogier 7 (3).
Vuillemier, B. 28 (1), 77 (2), 89 (6).
Wadsworth, R.K. 336 (3), 456 (3), 578 (3).
Wagner, R.J. 37 (3), 63 (2), 63A (2), 603 (3), 754 (2), 971 (3), 1248 (5), 1732 (2).
Weaver, R.A. 854 (1), 899 (6), 979 (6), 1093 (1), 1144 (1), 1225 (1), 1283 (6), 1802 (1), 1825 (1), 1950 (1).
Webster, G. 236 (1), 4081 (2), 5139 (8) 5269 (6), 5368 (6), 5391 (6), 5538 (2), 5614 (1), 5633 (6), 8029 (1), 8398 (6), 8443 (6), 8678 (3), 9510 (3), 9221 (3), 13649(6), 13544 (3).
West, H. 276 (6), 672 (1), 908 (6).
Wetmore, A. 162 (3).
Whitefoord, C. 1387 (6), 1397 (6), 3494 (3), 3695 (3), 3756 (3), 3760 (3), 3773 (3), 4564 (3), 5316 (3), 5421 (3), 5493 (3), 5494 (3), 5588 (3).
Wilbur, R.L. 7433 (3), 7525 (3), 7545 (3), 7712 (3), 7758 (3), 8187 (3), 8315 (3).
Wilson, K.A. 207 (3), 235 (3), 598 (1), 9834 (2).
Wolle 9 (6).
Woodbury, R.O. 647 (1).
Woods 11032 (6).
Wright, C. 172 (2), 210 (5), 229 (G, GH, K, P, MO, 2; NY, 7), 235 (1), 239 (1), 248 (1), 272 (1), 292 (2), 293 (5), 294 (2), 294B (2), 2756 (7).
Wullschlagel, H.R. 840 (6).
Wydler, H. 374 (3).
Yuncker, T.G. 17697 (1).
Zanoni, T.A. 11975 (2), 11992 (2), 12831 (5), 12871 (2), 15740 (2), 15914 (2), 16336 (2), 18661 (4), 19181 (4), 19224 (4), 20751 (3), 21343 (4), 21419 (4), 22186 (4), 22596 (1), 22289 (4), 23213 (4), 24892 (4), 24746 (3), 25766 (4), 26541 (4), 27586 (4), 26772-V (4), 29357 (3), 29385 (3), 30365 (4), 30863 (2), 30865 (4), 33195 (4), 34142 (2), 35789 (2), 36363 (1), 36504 (4), 37145 (4), 37412 (1), 37443 (4), 37767 (4), 39139 (4), 39821 (4), 42452 (4), 43960 (5).